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A REVISION OF THE ROVE BEETLE TRIBE  
FALAGRIINI OF AMERICA NORTH OF MEXICO  
(COLEOPTERA: STAPHYLINIDAE: ALEOCHARINAE)

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**Abstract.**—The species of the tribe Falagriini (Staphylinidae: Aleocharinae) of America north of Mexico are revised. Twenty-two species, representing nine genera, are recognized. Included in this total are three new species (type localities in parentheses): *Myrmecocephalus sculpturatus* (Cochise County, Arizona, USA), *M. gatineauensis* (Gatineau N. C. C. Park, Quebec, CANADA) and *Falagrioma socorroensis* (Socorro County, New Mexico, USA). One European species is reported for the first time from North America: *Falagria sulcata* (Paykull). The following species names are placed in synonymy: *Chitalia granulosa* Casey and *Chitalia illustris* Casey [= *Aleodorus scutellaris* (LeConte)]; *Lorinota bilimbata* Casey [= *Myrmecocephalus concinnus* (Erichson)]; and *Lorinota parva* Casey [= *Myrmecocephalus gracilis* (Casey)]. The genus group name *Omoschema* Notman is placed in synonymy with *Lissagria* Casey thus creating a new combination for the name *laticeps* Notman. Usage of the genus group name *Myrmecocephalus* MacLeay is briefly discussed. The following species names, previously considered to be junior synonyms, herein are recognized as valid: *Lorinota gracilis* Casey and *Lorinota pinalica* Casey (both now placed in *Myrmecocephalus*); and *Falagria scutellaris* LeConte (now placed in *Aleodorus*). The generic group names *Falagrioma* Casey and *Leptagria* Casey are also removed from synonymy (both with *Anaulacaspis* Ganglbauer). A neotype is designated for *Aleochara bilobata* Say and lectotypes are designated (when necessary) for the species described from America north of Mexico by Bernhauer, Casey, Erichson and LeConte. *Myrmecopora* Saulcy is excluded from the Falagriini.

Adults of all twenty-two species are described or redescribed. The male genitalia, female spermatheca, and other structures are illustrated with scanning electron photomicrographs and standard macro- and microphotographs. The distribution of each species in America north of Mexico is recorded and mapped, based on specimens examined. Diagnostic keys are provided for all genera and species occurring in America north of Mexico. Proposed phylogenetic relationships among the North American genera are presented and discussed. A checklist of genera and species of North American Falagriini is added.

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This paper is the first of a proposed series in which I plan to revise the genera and species of the Falagriini of the Western Hemisphere. The tribe Falagriini (sensu Seevers, 1978, in part) is cosmopolitan in distribution; there are over 215 species, representing at least 10 genera, recorded in the *Coleopterorum Catalogus* (Bernhauer and Scheerpeltz, 1926) and subsequent issues of *Zoological Record* (through 1979). In America north of Mexico the tribe is comprised of 9 genera and 22 species. Three species, representing 2 genera, herein are described as new.

The North American species of the tribe have been revised only once, by Casey in 1906. Unfortunately, his work now is antiquated and of no practical use in identifying the majority of the species. Since Casey, no attempt has been made to review the group. Recently published papers include descriptions of new taxa, and a few additional papers have presented keys to the world genera (Fenyès, 1912; Notman, 1920).

The present study is based entirely on the examination of adult specimens. The traditional morphological characters of the tribe have been thoroughly re-studied and all other available information on morphology, bionomics, geographical distribution, and phylogeny has been incorporated. In addition, the first detailed examination of male and female genitalia has been undertaken.

In America north of Mexico the Falagriini comprise a heterogeneous group of genera. Various taxa (i.e., *Lissagria*, *Leptagria*, *Falagrioma* and *Myrmecocephalus*) have been regarded at one time as subgenera of the once large genus *Falagria* Leach, but herein are recognized as distinct genera. The genus *Myrmecopora* Saulcy, historically regarded as a member of the Falagriini, does not belong to the tribe, and is excluded from this study; its placement remains unresolved at present, but it may prove closely aligned to the genus *Gnypeta* Thomson and related taxa of the Tachyusae (Oxypodini).

#### TAXONOMIC HISTORY

Although numerous papers have been published with descriptions of new species, few contribute to overall knowledge of North American Falagriini. Only the larger, more important papers are discussed below.

LeConte (1866) described 7 new North American species of the genus *Falagria*,



and provided a key to these and 3 previously described species. Two of his species (*vaga* and *cavipennis*) are now assigned to genera excluded from the Falagriini. The remaining 5 species are now assigned to falagriine genera other than *Falagria*.

Casey (1906) produced the first comprehensive study of the North American Falagriini. He proposed 8 new genera, 33 new species, and provided detailed keys to all taxa known from North America. Casey recognized the Falagriae as a subtribe of the Myrmedoniini. Casey described many new species from unique specimens, and in many instances, on the basis of only minor variation; he did not recognize morphological variation within species. Thus, many of Casey's names have been subsequently placed in synonymy.

Fenyés (1912) discussed the genus *Falagria* and its close relatives (excluding the group Tachysuae) in detail. He produced a key to the known world genera, provided a brief diagnosis of each genus, and assigned these genera to the tribe Myrmedoniini.

Notman (1920) gave a synopsis of the genera comprising the Falagriae, also presented a key to the known world genera, and proposed the new genus *Omoschema* based on the new species *laticeps* from Florida.

Also in 1920, Fenyés presented rather detailed descriptions of the world genera of the Aleocharinae, including those of the Falagriae; a checklist of the known world species for each genus was included.

Lohse (1974) proposed changes in the classification of the falagriine taxa. The Myrmedoniini (sensu Bernhauer and Scheerpeltz, 1926) was suppressed, and each of its component taxa (cited as subtribes) were elevated to rank of tribe.

Seevers (1978) incorporated additional changes in the higher classification of the Aleocharinae and provided the following comments on the position of the Falagriini. "In my opinion, the specialized parameres of the male genitalia of the Falagriini clearly set them apart from the Tachysuae. In my revised tribal system, in which the tribe Myrmedoniini is a much more restricted taxon and in which the Falagriini are accorded tribal status, the Tachysuae are assigned to the Oxypodini." Seevers stated that the precedent of classifying the Tachysuae with the Falagriae is unwarranted; the Tachysuae lack the specialized features of the Falagriini.

#### METHODS AND MATERIALS

This study is based on the examination of over 4,600 specimens on loan from numerous institutions and university collections, obtained by personal collecting, and from private collections of a few individuals.

Specimens were examined with a Wild M-5 binocular microscope. Because of their small size, the majority of the Falagriini are difficult to identify. Accurate identification requires careful examination of dorsal and ventral body surfaces, and the male and female genitalia. To observe the presence or absence of punctures, and the details of surface microsculpture, it is necessary to use high magnification (a minimum of 50 $\times$ ) and an intense light source. A light source directed through a screen of Mylar® film set immediately in front of the specimen provides a diffuse source of lighting and reduces reflection; this allows for close examination of fine surface details not otherwise visible.

Genitalia and terminalia (segments VIII–X) were examined by removing the apex of the abdomen and placing it in warm 10% KOH. After clearing, structures were

transferred to small glass genitalia vials containing glycerin (which are then pinned beneath the specimen), mounted in Canada balsam on small acetate strips, or mounted in Hoyer's medium on glass microscope slides. Slide-mounts of mouthparts, and genitalia and associated tergites and sternites were studied with the aid of a Leitz Dialux 20 research microscope. Photographs of these structures were made with an Olympus OM-2n camera mounted on a Wild M20 research microscope. Habitus photographs were made with the Olympus OM-2n mounted on an OM Auto bellows equipped with a Zuiko MC Macro (20 mm, F3.5) lens.

Examination of finer morphological characters was made possible by use of electron microscopy. Whole specimens were cleaned of most dust and debris with a fine camel-hair brush, then glued to the surface of standard SEM aluminum stubs. Specimens were coated with 250–300 Å of gold or gold paladium by a Balvers Union sputter coater. Photographs (4 × 5 Polaroid format) were taken with an AMR (Model 1000A) scanning electron microscope at various magnifications (usually under 250×) and at an accelerating voltage of 20 kV.

Body length was measured from the anterior margin of the head to the apex of the abdomen. Abdominal length may vary greatly because segments are capable of telescoping. For each species, adequate numbers of specimens were measured, when possible, to estimate range in length.

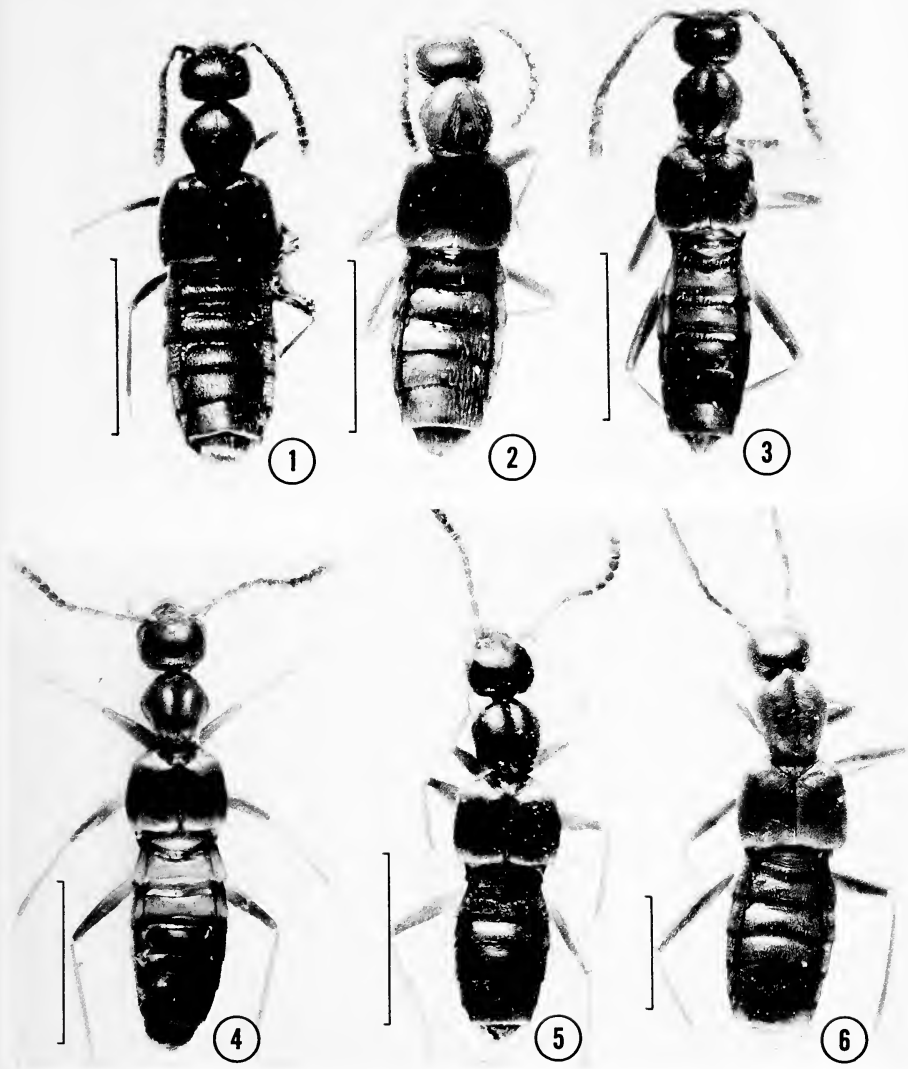
#### ANATOMICAL CHARACTERS

Anatomical characters of Falagriini are similar to those of other Staphylinidae and are outlined below using terminology of Blackwelder (1936) and Seevers (1978).

*Microsculpture.* Surface microsculpture of the head, pronotum, elytra and abdominal terga is of taxonomic value at the species level only in *Myrmecocephalus*. The pattern of microlines is constant for sclerites and species, and must be viewed using high magnification and an intense, diffuse light source (see Methods). Two sorts of microsculpture are recognized. Transverse microsculpture, the most common sort, consists of irregular transverse meshes of wavy microlines which is denser in some species (abdominal terga of *M. cingulatus*, *concinus*, *gracilis*, and *gatineauensis*), sparser in others (abdominal terga of *M. caviceps* and *pinalicus*). Reticulate microsculpture consists of a network of fine, fused lines forming an isodiametric (pentagonal or hexagonal) pattern, as seen in *M. sculpturatus*. In *M. arizonicus* and specimens of all other genera of the tribe in America north of Mexico, there is no apparent surface microsculpture.

*Punctuation and pubescence.* All body surfaces are finely or coarsely punctured and pubescent. The head is very finely punctured and sparsely pubescent. Pronotal punctuation varies among taxa, from very fine (*Cordalia*, *Falagriota*, *Myrmecocephalus* and *Borboropora*) to very dense, coarse, and often asperate (*Aleodorus*); the pubescence is uniform and moderate to dense. Elytral punctuation is either uniform (*Falagria*, *Myrmecocephalus*, *Falagriota* and *Leptagria*) or very dense, coarse, and often asperate near the scutellum (*Aleodorus*, *Borboropora*, *Falagrioma* and *Lissagria*). Elytral pubescence is uniform and moderate to dense. The terminal abdominal terga are more densely and closely but less asperately punctured than the basal terga.

*Head.* The head is abruptly constricted behind, forming a distinct neck. Its most important characters are shape and relative size.



Figs. 1-6. Habitus, dorsal aspect. 1. *Cordalia obscura*. 2. *Falagriota occidua*. 3. *Myrmeccephalus cingulatus*. 4. *M. concinnus*. 5. *M. gracilis*. 6. *M. sculpturatus*. All scale lines = 1.0 mm.

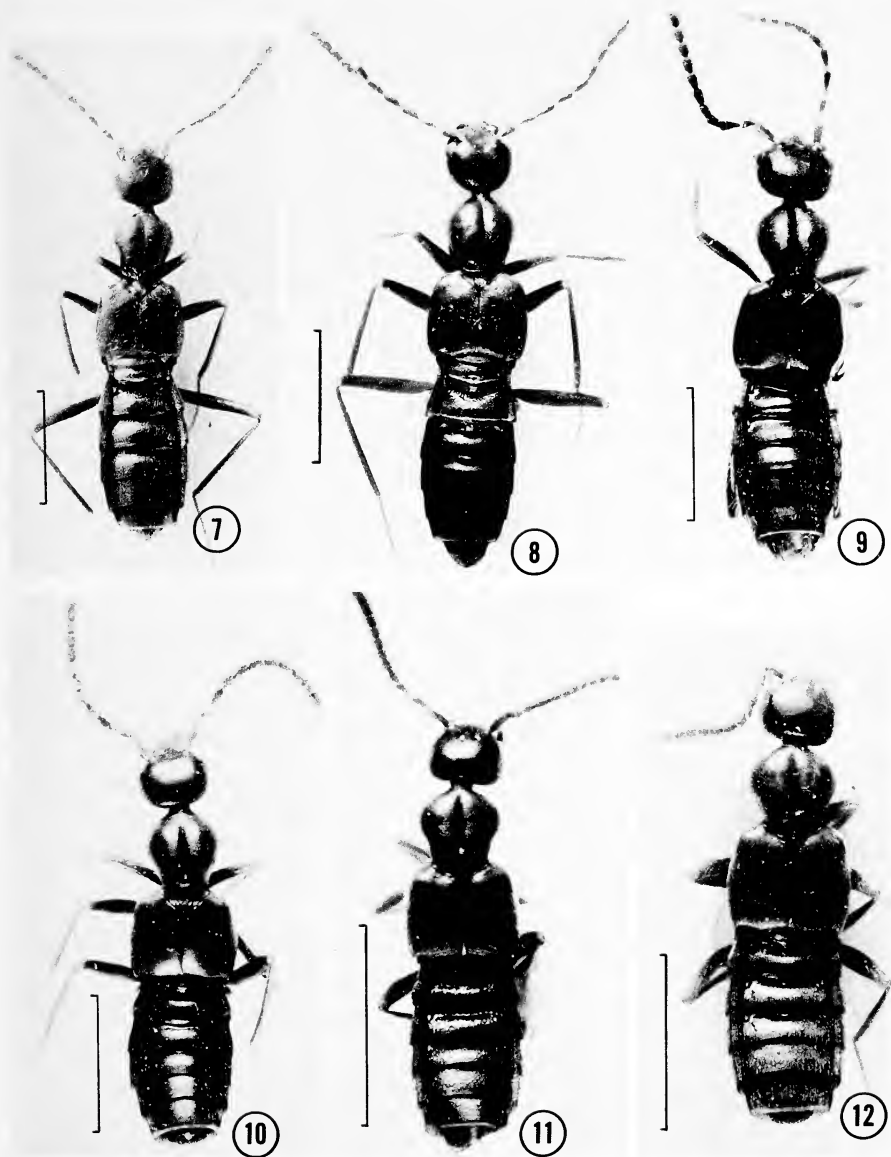


*Mouthparts.* Slight variation is found in mouthparts of the Falagriini. The labrum is large, transverse and strongly setose, with the anterior margin rounded to subtruncate. Mandibles are robust or elongate, slender and prominent (*Borboropora*). The inner margin of the right mandible is with or without teeth; the inner surface of the left mandible is simple. The maxilla is uniform in structure, with size and shape of the cardo, stipes, galea and lacinia subject to little variation. The galea is as long as or longer than the lacinia and densely pubescent at the membranous apex. The lacinia is feebly curved apically, with apex attenuate and hooked; the apical half or third is armed with a brush of long to short spines on the mesal surface, and sparsely to densely pubescent below the spines. The maxillary palpus is 4-segmented, slender and elongate. Segment 3 is longer, and usually broader than 2, with the apical half incrassate. Segment 4 is long, narrow, and subuliform. The mentum is transverse and narrowed towards the front, with the anterior margin emarginate to subtruncate. The ligula is long, deeply bifid, and shorter than segment 1 of the labial palpus. The labial palpus is 3-segmented, elongate. Segment 1 is long and broad. Segment 2 is very short and narrower than 1. Segment 3 is longer than 2 and truncate at the apex.

*Pronotum.* Considerable variation is found in the dorsal aspect of the pronotum. In nearly all members of the tribe, the pronotum narrows appreciably at the base, and is deeply sulcate along the median line in specimens of all species except *Falagriota occidua* and *Cordalia obscura*. In specimens of some genera, the hypomera (the inflexed portion of the pronotum) is set off or delimited from the disc by a marginal ridge or carina. The hypomera varies from long and narrow (*Myrmecocephalus*) to short and dilated at the middle (*Falagria*, *Falagrioma*, *Leptagria* and *Falagriota*). The marginal ridge is completely absent in *Cordalia*, *Aleodorus*, *Lissagria* and *Borboropora* and the hypomera is indistinguishable from the disc of the pronotum. The ventral aspect of the prothorax includes the elongate sternum; the hypomera; and a pair of usually enlarged, heavily sclerotized mesospiracular plates or peritremes. These peritremes, which support the mesothoracic spiracles, are large, quadrate and contiguous in *Aleodorus*, *Falagria*, *Cordalia* and *Myrmecocephalus*, or ovoid, slightly separated in *Lissagria*. In *Falagriota*, these sclerites are reduced in size and widely separated, exposing a greater amount of membrane.

*Mesosternum and metasternum.* Sternal elements of the pterothorax provide important taxonomic characters. The posterior margin of the mesosternum is prolonged at the middle as a broad to narrow median lobe (mesosternal process), partially separating the mesocoxae. When viewed from below, the mesosternum and metasternum are on the same level or plane in all genera, except in *Aleodorus* where the mesosternum is elevated above the metasternum (Fig. 79). The metasternum is represented by a large, broad sclerite whose anterior margin at the median line projects forward between the mesocoxae as a broad lobe. In most genera the intercoxal processes are separated by a short, and sometimes depressed, isthmus. Intercoxal processes vary in length, width, convexity, and degree of separation. Mesocoxal cavities are moderately separated and usually not delimited posteriorly. In *Cordalia*, however, the posterior aspects of the mesocoxal acetabula are defined by a fine bead, raised line (Fig. 76).

*Scutellum.* The scutellum is simple, flat or convex, densely and coarsely punctured in *Leptagria*, *Falagriota*, *Lissagria* and *Borboropora* and some species of *Aleodorus*;



Figs. 7-12. Habitus, dorsal aspect. 7. *Myrmecocephalus arizonicus*. 8. *M. gatineauensis*. 9. *M. caviceps*. 10. *M. pinalicus*. 11. *Falagria dissecta*. 12. *F. sulcata*. All scale lines = 1.0 mm.

flat with a broad to narrow, and sometimes incomplete, impressed channel in some species of *Aleodorus* and in *Falagrioma*; completely or incompletely unicarinate along the median line in *Myrmecocephalus*; and bicarinate in *Falagria*.

*Elytra*. The elytra offer few diagnostic characters. Punctuation and pubescence is generally evenly and uniformly distributed over the surface of the disc, but in some taxa the punctuation and pubescence is much more dense near the scutellum (see Punctuation and Pubescence). Elytra are generally longer than the prothorax, except in *Falagriota occidua* where some individuals have reduced and shortened elytra.

*Abdomen*. The abdomen is 10-segmented and telescopic as in other Staphylinidae. It is constricted at the base, and not quite as broad at the base as the elytra. Abdominal terga III–V are transversely impressed at the base, with the impressions variously punctured and sculptured or smooth and impunctate.

*Terminalia*. The tergites and sternites of segments VIII and IX and the tergum of segment X are here defined as the terminalia. Segment VIII consists of a tergum and sternum only. Segments IX and X are modified in relation to the genitalia and show little modification from the typical structure found in other Staphylinidae (see Blackwelder, 1936). There is a virtual absence of secondary sexual characters in most Falagriini. Only the male has a ninth abdominal sternite, and this provides the only external means of identifying the sexes. However, in most dried specimens the apex of the abdomen is telescoped, making it impossible to determine the sex without relaxing them. In some members of the tribe the apical margin of tergum VIII is simple and unmodified (*Falagriota* and *Myrmecocephalus*) while in others the apical margin is either emarginate and densely fimbriate (*Cordalia*), or minutely denticulate (*Falagria*, *Leptagria*, *Falagrioma*, *Aleodorus*, *Lissagria* and *Borboropora*). Sternum VIII is unmodified except in the female of *Myrmecocephalus concinnus* where the apex is deeply notched at the middle.

*Male genitalia*. Characters of the male genitalia are important in distinguishing genera and species. The genitalia consist of a tubular median lobe, which is bulbous basally, and two parameres. The membranes of the internal sac are adorned with variously shaped accessory structures (plates and spinules). A flagellum is present or absent. As in other Aleocharinae, the parameres are large, expansive structures. Each paramere, consisting of the condylite and paramerite, articulates with the median lobe by condyles distad to the median foramen. The apical lobe of the paramerite varies in shape, length and chaetotaxy. The parameres of members of the Falagriini are distinctive: the velum of the condylite is clearly separated from that of the paramerite, a condition shared only with the Sceptobiini (Seevers, 1978:148).

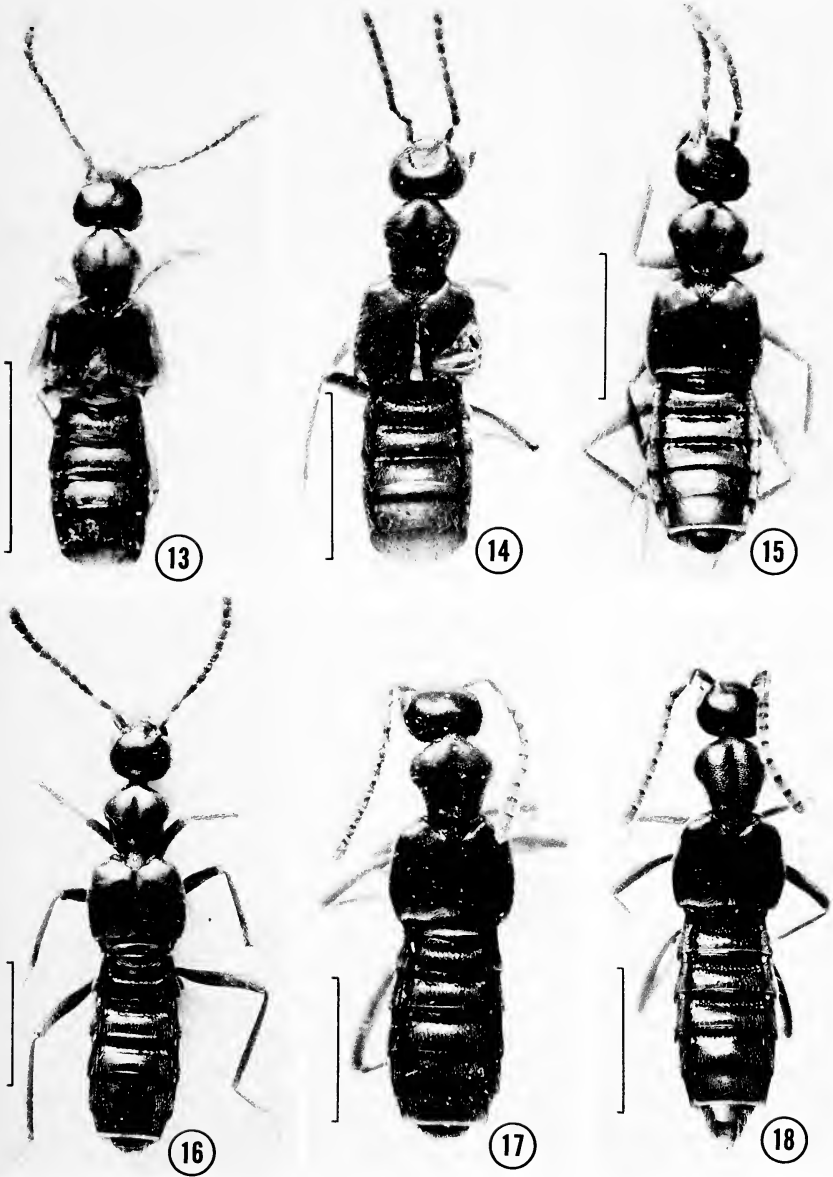
*Female genitalia*. The female genitalia are simple and unsclerotized. Shape of the heavily sclerotized spermatheca (and sometimes spermathecal duct) is an important character at the species level, though subject to some minor intraspecific variation.

#### SYSTEMATICS

##### Tribe Falagriini

Falagriae Erichson, 1840, p. 34; Casey, 1906, p. 183 (ex parte); Fenyès, 1918, p. 18; Leng, 1920, p. 124 (ex parte); Notman, 1920, p. 730 (ex parte); Bernhauer and Scheerpeltz, 1926, p. 571 (ex parte); Scheerpeltz, 1929, p. 9 (ex parte); Bradley,





Figs. 13–18. Habitus, dorsal aspect. 13. *Leptagria perexilis*. 14. *Falagrioma socorroensis*. 15. *Aleodorus partitus*. 16. *A. intricatus*. 17. *A. scutellaris*. 18. *A. bilobatus*. All scale lines = 1.0 mm.

1930, p. 85; Scheerpeltz, 1934, p. 1568 (ex parte); Blackwelder, 1944, p. 158 (ex parte); Hansen, 1954, p. 95 (ex parte); Palm, 1968, p. 75 (ex parte); Scheerpeltz, 1974, p. 51, 221 (ex parte).

Falagriates Mulsant and Rey, 1875, p. 428; Ganglbauer, 1895, p. 107.

Falagriini Horion, 1967, p. 198 (ex parte); Lohse, 1974, pp. 15, 64 (ex parte); Seevers, 1978, p. 143 (excl. *Myrmecopora*).

Falagrina Arnett, 1968, p. 288 (ex parte).

*Diagnosis.* In addition to the characters shared by other Staphylinidae and, in particular other Aleocharinae, members of the tribe Falagriini are characterized by the following features.

Staphylinidae (Aleocharinae) of very small size, generally much less than 4.0 mm (most 2.0–3.5 mm in length), narrow and elongate form, most specimens convex or slightly depressed.

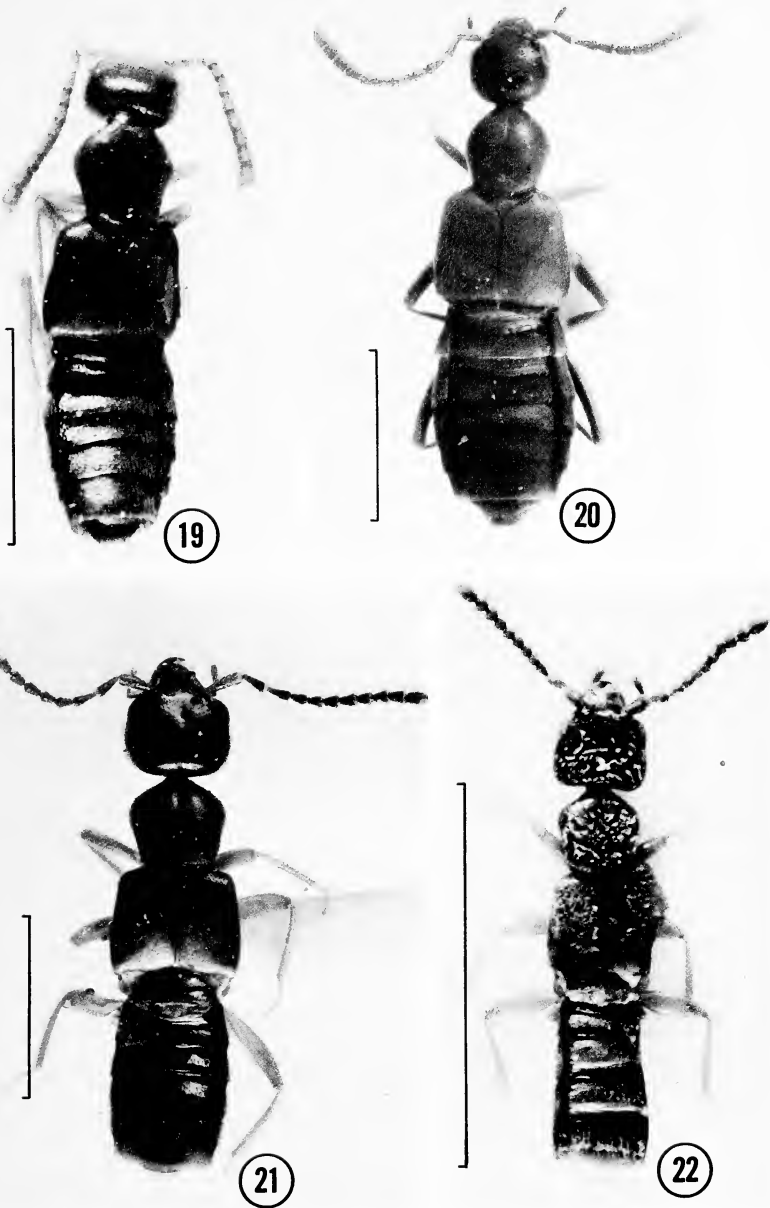
Head moderate to large, variously shaped from rounded to quadrate, with a distinctly constricted neck, less than  $\frac{1}{3}$  as wide as the head in most specimens. Antenna 11-segmented. Lacinia of maxilla spinose at apex and ciliate along inner margin. Galea finely and densely ciliate on membranous apex. Maxillary palpus 4-segmented. Labial palpus 3-segmented. Ligula bifid.

Prothorax narrowed at base; base not more than  $\frac{3}{4}$  of the maximum width; disc with distinct sulcus along median line in most specimens (sulcus faint in *Falagriota* and *Cordalia*), ending in a round or transverse fovea. Prosternum elongate before and behind procoxae; mesospiracular plates or peritremes behind each procoxa usually extremely enlarged and heavily sclerotized (peritremes smaller in *Falagriota*). Inflexed hypomera of pronotum either delimited by a marginal ridge or not. Procoxal cavities functionally "closed" by the elongated prosternum, hypomera, and enlarged mesospiracular peritremes. Mesocoxal cavities moderately separated. In most genera the mesosternum and metasternum are on the same level; however, in *Aleodorus* the posterior margin of the mesosternum is on a level or plane ventral to the metasternum, and the mesosternal process is very short.

Scutellum usually large, triangular and variously sculptured (variation discussed under each generic section).

Elytra usually at least  $\frac{1}{4}$  longer than prothorax, convex, sides subparallel, broadly arcuate posteriorly, posterior margins broadly sinuate at outer angles. Elytra shortened in some individuals of *Falagriota occidua*. Disc uniformly punctured and pubescent (*Falagria*, *Falagriota*, *Cordalia*, *Leptagria*, and *Myrmecocephalus*), or with area of dense and coarse punctation and pubescence near scutellum (*Aleodorus*, *Borboropora*, *Lissagria* and *Falagrioma*). Dorsal surface between punctures smooth and shining (most species of the tribe) or with fine surface microsculpture (most species of *Myrmecocephalus*).

Abdomen broad and slightly constricted at base, not quite as broad as elytra at apex. Terga III–V usually broadly, transversely and deeply impressed at base; impressions smooth, or coarsely sculptured and punctate. Apical margin of tergum VIII with an arcuate comb of minute denticles (*Leptagria*, *Falagria*, *Falagrioma*, *Lissagria*, *Borboropora* and *Aleodorus*), densely fimbriate (*Cordalia obscura*), or simple and unmodified (*Falagriota* and *Myrmecocephalus*).



Figs. 19–22. Habitus, dorsal aspect. 19. *Lissagria laticeps*. 20. *L. laeviuscula*. 21. *Borboropora quadriceps*. 22. *B. sulcifrons*. All scale lines = 1.0 mm.

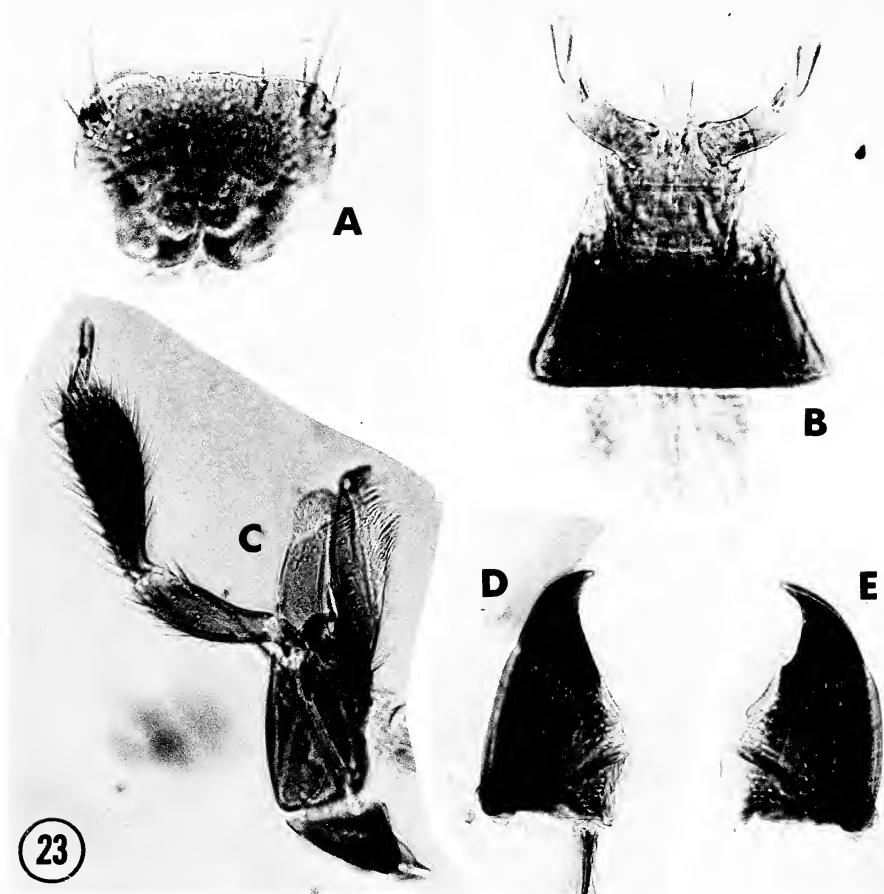


Fig. 23. Mouthparts of *Cordalia obscura*. A. Labrum. B. Labium. C. Maxilla. D. Left mandible. E. Right mandible.

Legs generally long and slender; hind tarsus elongate,  $\frac{2}{3}$  to equal in length to tibia; segment 1 subequal in length to 2-3 or 2-4 combined. Tarsal formula 4,5,5.

Median lobe of aedeagus variously shaped in profile, but with a bulbous base and tubular apex; internal sac with various accessory structures (plates and spinules), with or without a flagellum; paramere large, distinctive and unique: condylite velum clearly separated from paramerite velum.

Spermatheca heavily sclerotized and variously shaped.

*Remarks.* *Myrmecopora* Saulcy, containing only a single species (*vaga*) in America north of Mexico, herein is removed from the Falagriini. The characters by which it is excluded are the broad neck of the head capsule; the pronotum not narrowed

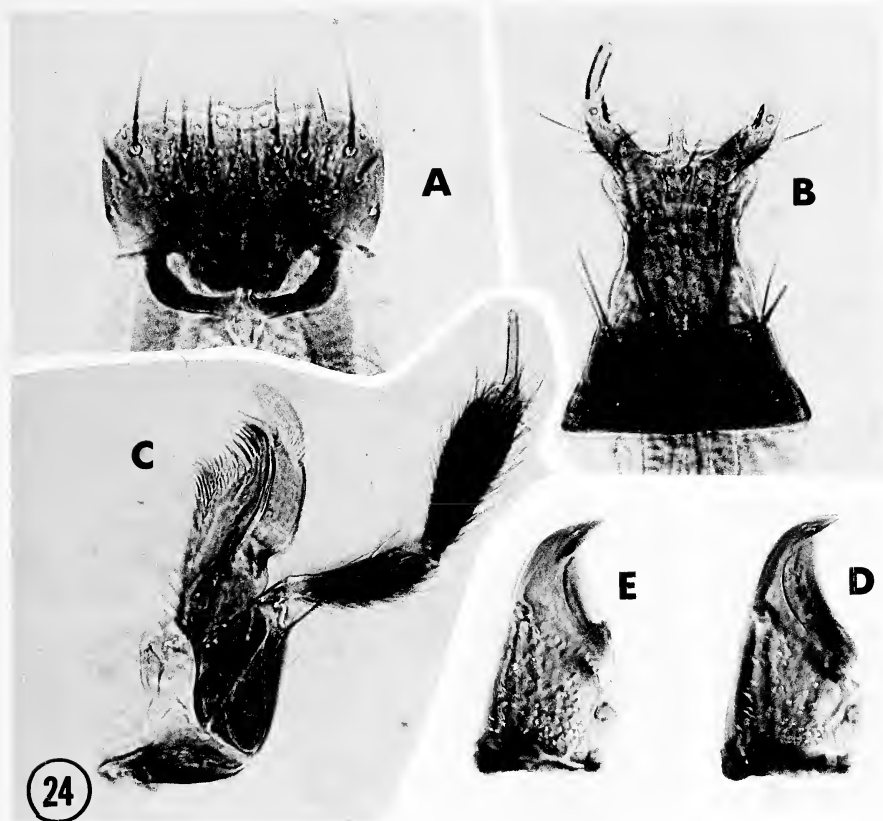


Fig. 24. Mouthparts of *Falagriota occidua*. A. Labrum. B. Labium. C. Maxilla. D. Left mandible. E. Right mandible.

behind the middle; the lack of a defined median sulcus of the pronotum; the small, corset-like mesospiracular peritremes; and the velum of the paramerite confluent with that of the condylite.

North American aleocharines closely resembling, and likely to be confused with, the Falagriini include members of the tribes Oxypodini (subtribes Tachysusae and Blepharhymeni) and Autaliini. The Tachysusae previously have been closely aligned to the Falagriini because of the similar habitus of some members and the shared 4,5,5 tarsal formula (Bernhauer and Scheerpeltz, 1926 and others), but they lack the specialized features of the Falagriini. Members of the Tachysusae have the condylite velum (of the male paramere) confluent with the paramerite velum; pronotum not narrower at base than apex; pronotum without a distinct median sulcus; and pro-sutal membrane without enlarged, heavily sclerotized mesospiracular peritremes. The Blepharhymeni (including the sole North American genus *Blepharhymenus*), although closely resembling many *Tachysus* in overall appearance (especially ab-



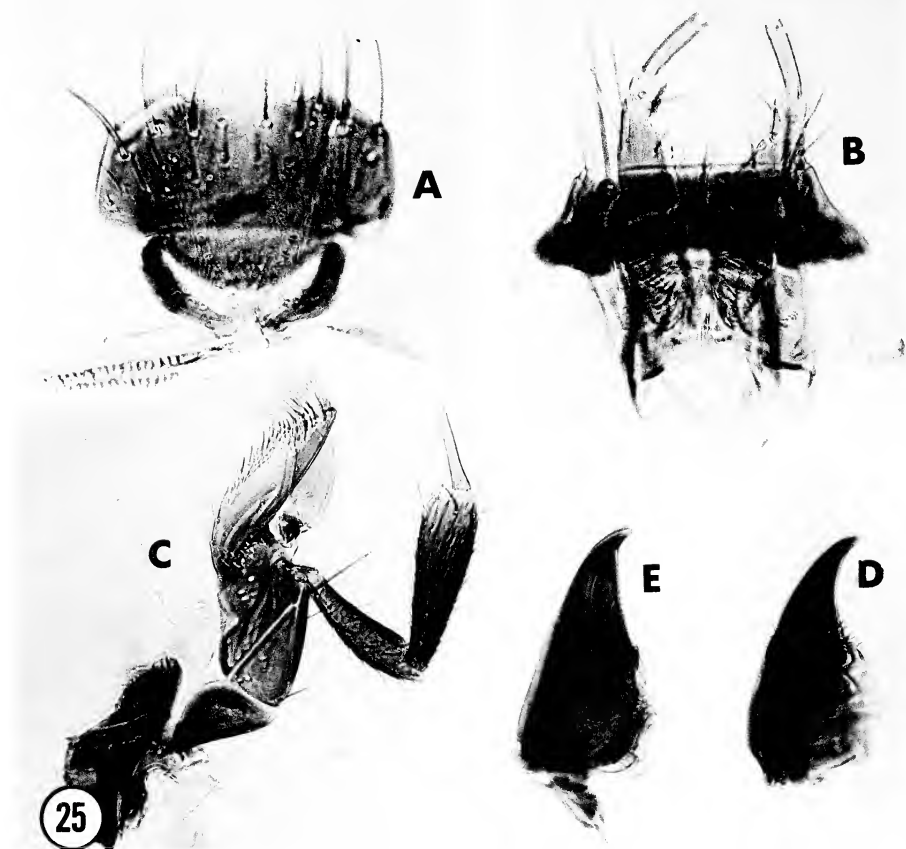


Fig. 25. Mouthparts of *Myrmecocephalus cingulatus*. A. Labrum. B. Labium. C. Maxilla. D. Left mandible. E. Right mandible.

dominal characteristics), have a 5,5,5 tarsal formula and a moderately broad neck of the head capsule. Like the Falagriini, the Autaliini (with the single genus *Autalia* in North America) have a head capsule with a very slender neck and a distinctive habitus. However, species of *Autalia* are differentiated from the Falagriini by a 4,4,5 tarsal formula, the pronotum with four subbasal foveae, and each elytron with two conspicuous basal foveae.

To distinguish the Falagriini from other myrmedoniine-related tribes, a key by Kistner (1972) should be consulted, and also the work of Seevers (1978).

#### CHECKLIST OF THE FALAGRIINI OF AMERICA NORTH OF MEXICO

The species listed below (and synonymies) have been arranged alphabetically for each genus and do not necessarily reflect relationship. For each taxon, reference is given for the original description only.

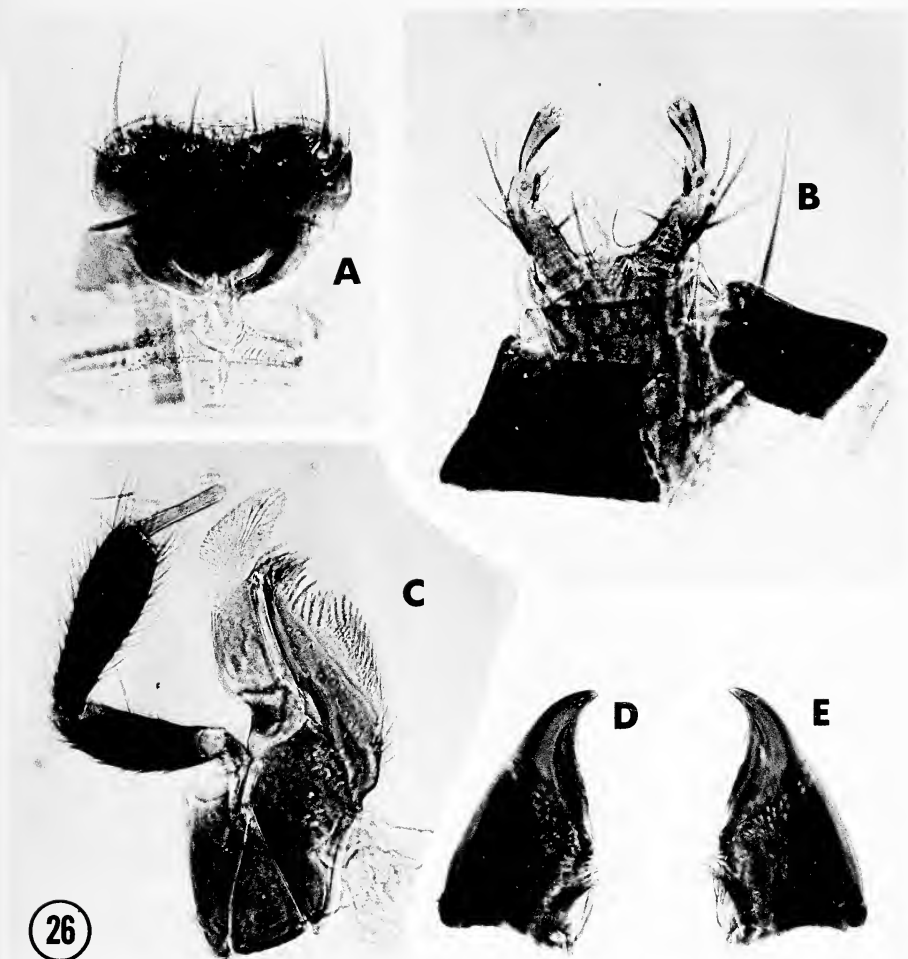


Fig. 26. Mouthparts of *Falagria dissecta*. A. Labrum. B. Labium. C. Maxilla. D. Left mandible. E. Right mandible.

FALAGRIINI Erichson, 1840:34

*Cordalia* Jacobs, 1925:82

*Cardiola* Mulsant and Rey, 1874:38

*Cardiolita* Strand, 1933:123

*Strandiodes* Bernhauer, 1930:191

*Falagria auctorum* (in part)

*obscura* (Gravenhorst, 1802:74)

*crassiuscula* (Hochhuth, 1871:87)

*flavipes* (Stephens, 1832:105)

*floralis* (Stephens, 1832:105)

*immunis* (Stephens, 1832:129)

*nitens* (Stephens, 1832:105)

*Falagriota* Casey, 1906:255

*occidua* (Casey, 1885:285)

*asperula* Casey, 1906:257

*collaris* Casey, 1906:258

*evanescens* Casey, 1906:258

*lucida* Casey, 1906:257

*parvipennis* Casey, 1906:259

*picina* Casey, 1906:257

*Myrmecocephalus* MacLeay, 1873:134

*Lorinota* Casey, 1906:238

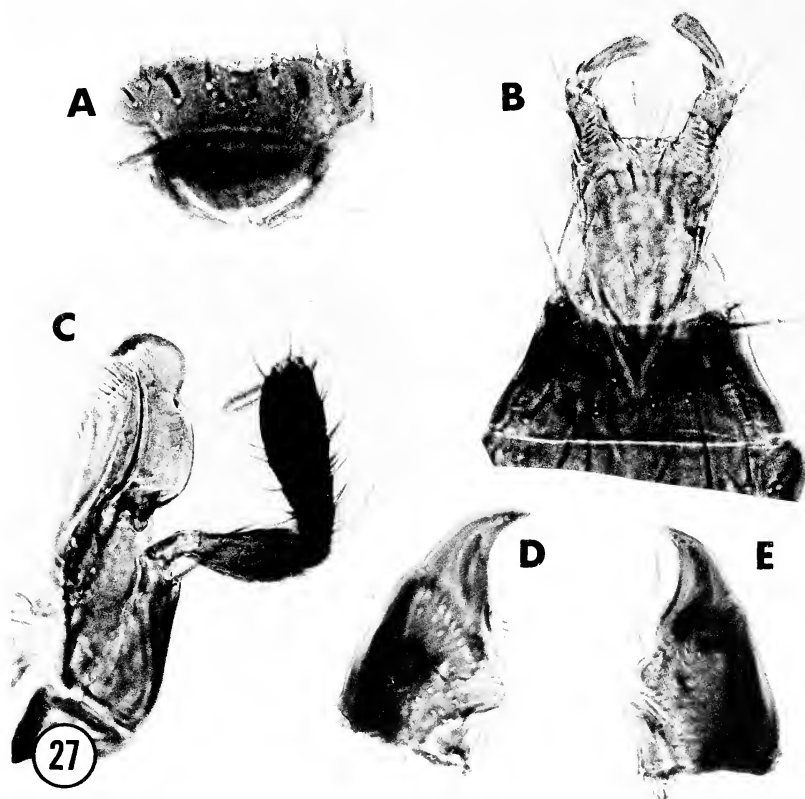


Fig. 27. Mouthparts of *Leptagria perexilis*. A. Labrum. B. Labium. C. Maxilla. D. Left mandible. E. Right mandible.

*Stenagria* Sharp, 1883:237  
*Stiliciodes* Broun, 1880:95  
*arizonicus* (Casey, 1906:241)  
*acomana* (Casey, 1906:242)  
*fontinalis* (Casey, 242)  
*caviceps* (Casey, 1906:240)  
*cingulatus* (LeConte, 1866:370)  
*sinuosa* (Casey, 1911:178)  
*tenuicornis* (Casey, 1906:243)  
*concinus* (Erichson, 1840:51)  
*bilimbata* (Casey, 1906:245), **New**  
**Synonym**  
*currax* (Sharp, 1880:37)  
*fovea* (Sharp, 1874:3)

*longipes* (Wollaston, 1871:284)  
*parae* (Sharp, 1876:41)  
*gatineauensis* Hoebeke, **New Species**  
*gracilis* (Casey, 1906:244), **Revised**  
**Status**  
*parva* (Casey, 1906:244), **New**  
**Synonym**  
*pinalicus* (Casey, 1906:241), **Revised**  
**Status**  
*sculpturatus* Hoebeke, **New Species**  
*Falagria* Leach, 1819:177  
*Coenobiotes* Gistel, 1856:387  
*dissecta* Erichson, 1840:49  
*angulata* Casey, 1906:249

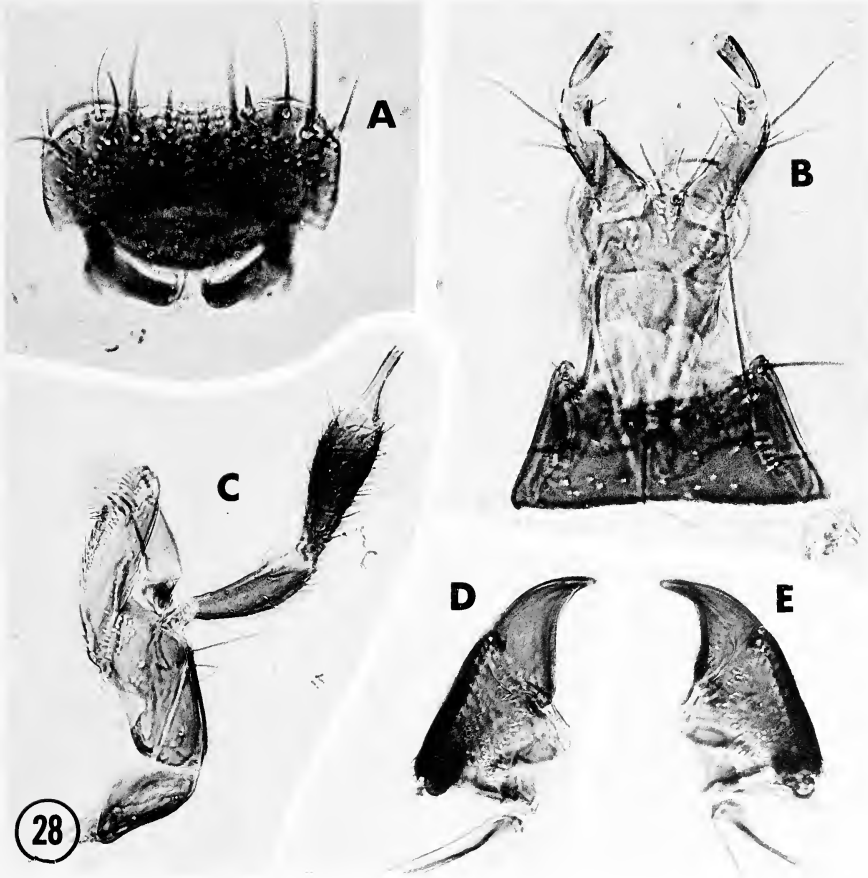


Fig. 28. Mouthparts of *Falagrioma thoracica*. A. Labrum. B. Labium. C. Maxilla. D. Left mandible. E. Right mandible.

*erythroptera* Melsheimer, 1846:30  
*globosa* Melsheimer, 1846:30  
*iowana* Casey, 1906:247  
*ithacana* Casey, 1906:247  
*sterilis* Casey, 1911:178  
*subsimilis* Casey, 1906:248  
*texana* Casey, 1906:248  
*sulcata* (Paykull, 1789:32)  
*caesa* Erichson, 1839:295  
*sicula* Jekel, 1873:33  
*Leptagria* Casey, 1906:227, **Revised Status**

*perexilis* Casey, 1906:250  
*hudsonica* Casey, 1906:251  
*Falagrioma* Casey, 1906:230, **Revised Status**  
*Anaulacaspis auctorum* (in part)  
*Falagria auctorum* (in part)  
*socorroensis* Hoebeke, **New Species**  
*Aleodorus* Say, 1830:60  
*Chitalia* Sharp, 1883:235  
*bilobatus* (Say, 1830:60)  
*canadensis* (Casey, 1906:236)  
*nigrescens* (Casey, 1906:236)

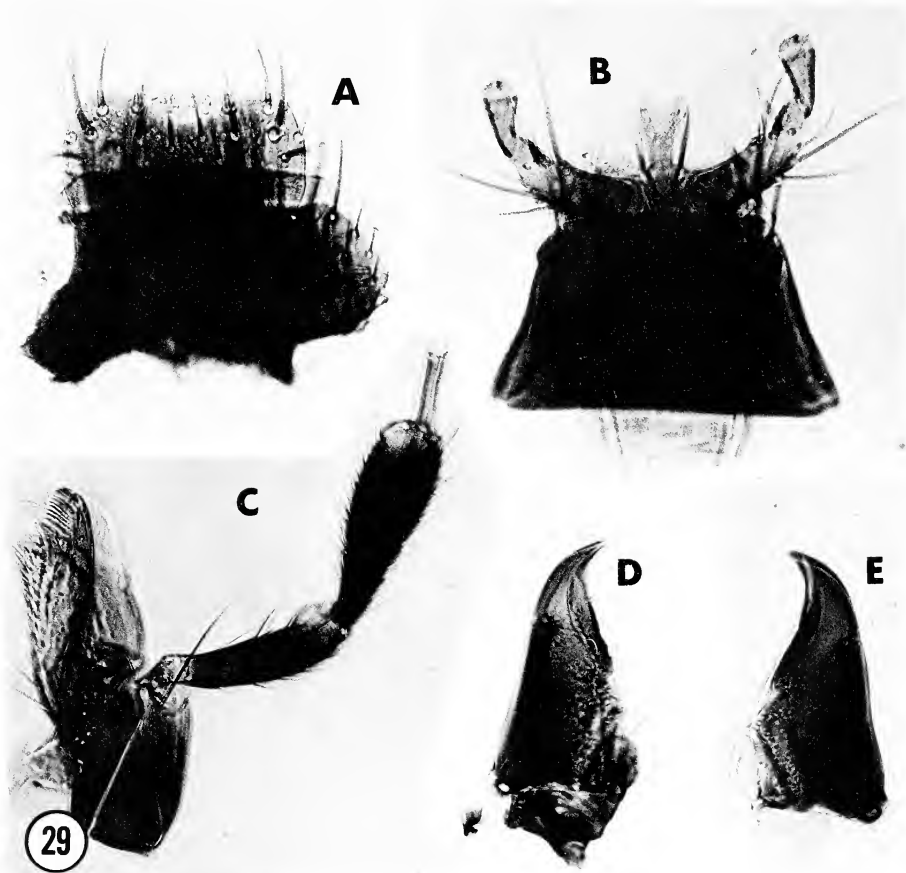


Fig. 29. Mouthparts of *Aleodorus bilobatus*. A. Labrum. B. Labium. C. Maxilla. D. Left mandible. E. Right mandible.

*turbata* (Casey, 1911:176)  
*intricatus* (Casey, 1906:234)  
*partitus* (LeConte, 1866:371)  
*floridana* (Casey, 1906:237)  
*novella* (Casey, 1911:176)  
*scutellaris* (LeConte, 1866:370), **Re-**  
**vised Status, New Combination**  
*granulosa* (Casey, 1906:235), **New**  
**Synonym**  
*illustris* (Casey, 1906:235), **New**  
**Synonym**

*Lissagria* Casey, 1906:252

*Omoschema* Notman, 1920:731,  
**New Synonym**  
*laeviuscula* (LeConte, 1866:371)  
*fissilis* Casey, 1906:254  
*impressifrons* Casey, 1906:254  
*longicollis* Casey, 1906:255  
*minuscula* Casey, 1906:254  
*robusta* Casey, 1906:254  
*laticeps* (Notman, 1920:732), **New**  
**Combination**  
*Borboropora* Kraatz, 1862:405  
*Aneurota* Casey, 1893:347



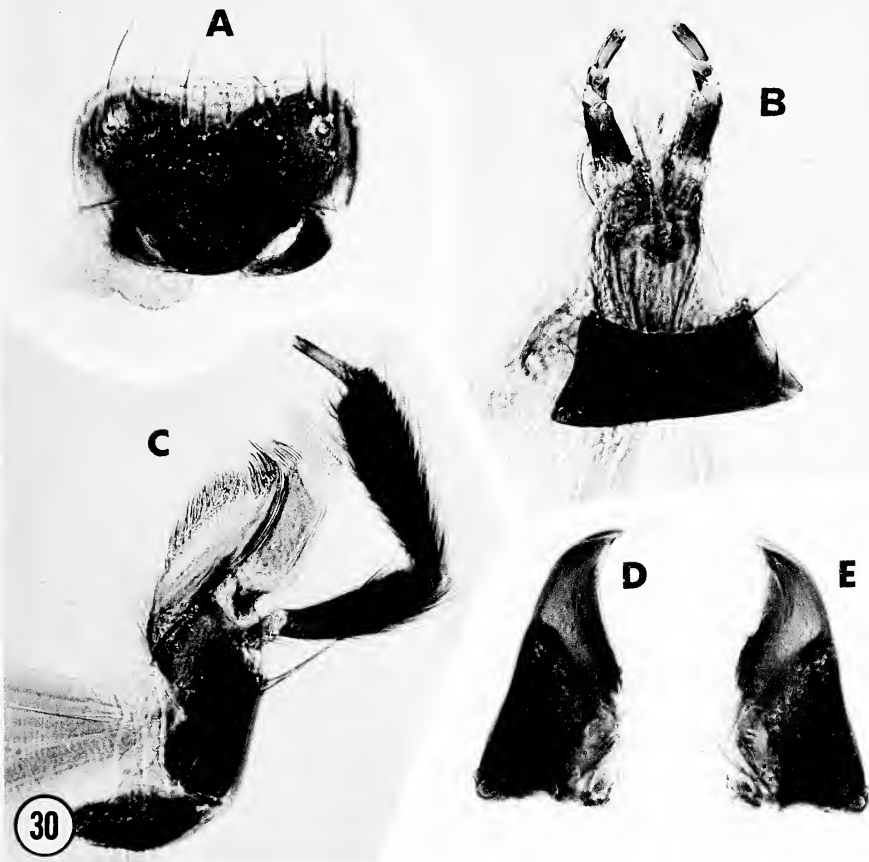


Fig. 30. Mouthparts of *Lissagria laeviuscula*. A. Labrum. B. Labium. C. Maxilla. D. Left mandible. E. Right mandible.

*Orthagria* Casey, 1906:260  
*Pseudoscopaeus* Weise, 1877:8  
*quadriceps* (LeConte, 1866:371)

*grandis* Bernhauer, 1905:21  
*sulcifrons* (Casey, 1893:348)

KEY TO GENERA OF FALAGRIINI OF AMERICA  
NORTH OF MEXICO

- 1. Mesospiracular peritremes large, quadrangular or ovoid (Figs. 79, 80); pronotum moderately to deeply sulcate (Figs. 34–38) ..... 2
- Mesospiracular peritremes smaller (Fig. 77); pronotum very faintly sulcate (Fig. 33) ..... 2. *Falagriota* Casey

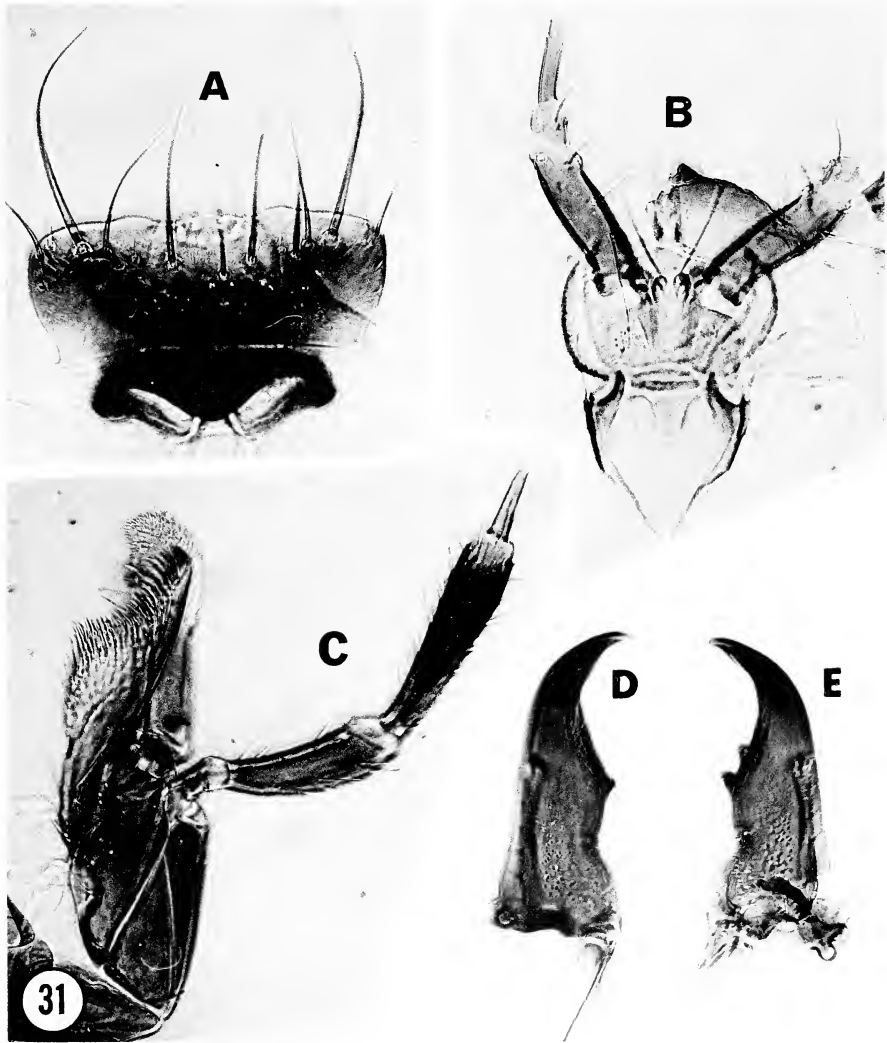


Fig. 31. Mouthparts of *Borboropora quadriceps*. A. Labrum. B. Labium. C. Maxilla. D. Left mandible. E. Right mandible.

- 2. Elytral punctation dense near scutellum (Figs. 48–50); apical margin of tergum VIII with arcuate comb of minute denticles (Figs. 72–75) ..... 3
- Elytral punctation not dense near scutellum, uniform throughout (Fig. 47); apical margin of tergum VIII with or without comb of denticles, or densely fimbriate (Fig. 70) ..... 6
- 3. Hypomera delimited from disc of pronotum by marginal ridge (Figs. 40, 41) ..... 6. *Falagrioma* Casey
- Hypomera not delimited from disc of pronotum (Figs. 42, 43) ..... 4
- 4. Mesosternum on a level ventral to the metasternum (Fig. 79); mesosternal process short, acute, not extended between mesocoxal cavities ..... 7. *Aleodorus* Say

- Mesosternum on the same level as the metasternum (Figs. 78, 80); mesosternal process longer, partially separating mesocoxal cavities ..... 5
- 5. Head large, subquadrate, with a median, longitudinal impression on anterior half of vertex in most specimens (Figs. 21, 22) ..... 9. *Borboropora* Kraatz
- Head not large, rounded or transverse; vertex without median, longitudinal impression ..... 8. *Lissagria* Casey
- 6. Mesocoxal acetabula margined posteriorly by fine bead, raised line (Fig. 76); apical margin of tergum VIII densely fimbriate (Fig. 70); each elytron at base with small, but distinct depression near humeral angle ..... 1. *Cordalia* Jacobs
- Mesocoxal acetabula not margined posteriorly; apical margin of tergum VIII with or without comb of minute denticles; each elytron at base without depression near humeral angle ..... 7
- 7. Apical margin of tergum VIII without denticles, simple (Fig. 71); scutellum with median longitudinal carina (complete or incomplete) (Fig. 34) .... 3. *Myrmecocephalus* MacLeay
- Apical margin of tergum VIII with comb of very minute denticles (Fig. 72); scutellum not as above (Figs. 44-46) ..... 8
- 8. Scutellum bicarinate (Figs. 35, 44) ..... 4. *Falagria* Leach
- Scutellum coarsely granulose (Fig. 36), with narrow, smooth, median impression, without carinae ..... 5. *Leptagria* Casey

1. *Cordalia* Jacobs

*Cardiola* Mulsant and Rey, 1874, p. 38 [junior homonym of *Cardiola* Broderip, 1834]; Casey, 1906, pp. 224, 231; Reitter, 1909, p. 75; Fenyés, 1912, pp. 20, 21, 25; Notman, 1920, p. 731; Fenyés, 1920, p. 147; Everts, 1922, p. 104; Bernhauer and Scheerpeltz, 1926, p. 572; Portevin, 1929, pp. 253, 294; Blackwelder, 1952, p. 93.

As subgenus of *Falagria*: Ganglbauer, 1895, p. 255; Everts, 1898, p. 231; Johansen, 1914, p. 241; Porta, 1926, p. 150.

Variant spelling: *Cardicola* Duvivier, 1883, p. 93.

*Type-species: Aleochara obscura* Gravenhorst, fixed by monotypy (Mulsant and Rey, 1874:38).

*Cordalia* Jacobs, 1924 (1925), p. 82 (=new name for *Cardiola* Mulsant and Rey, *nec* Broderip, 1834); Scheerpeltz, 1929, p. 9; 1930, p. 73; 1934, p. 1568; Cameron, 1939, pp. 233, 235; Tottenham, 1949, p. 387; Horion, 1951, p. 168; Blackwelder, 1952, p. 107; Hansen, 1954, p. 100; Horion, 1967, p. 199; Arnett, 1968, p. 288; Palm, 1968, p. 78; Scheerpeltz, 1974, pp. 51, 221; Moore and Legner, 1975, p. 390; SeEVERS, 1978, p. 146.

*Type-species: Aleochara obscura* Gravenhorst, through objective synonymy with *Cardiola*.

*Strandiodes* Bernhauer, 1930, p. 191 (=unnecessary new name for *Cardiola* Mulsant and Rey); Blackwelder, 1952, p. 364.

*Type-species: Aleochara obscura* Gravenhorst, through objective synonymy with *Cardiola*.

*Cardiolita* Strand, 1933, p. 123 (=unnecessary new name for *Cardiola* Mulsant and Rey); Blackwelder, 1952, p. 94.

*Type-species: Aleochara obscura* Gravenhorst, through objective synonymy with *Cardiola*.

*Falagria auctorum* (ex parte): Mannerheim, 1831, p. 87; Boisduval and Lacordaire,

1836, p. 556; Erichson, 1839, p. 295; 1840, p. 54; Heer, 1839, p. 351; Redtenbacher, 1849, p. 651; Fairmaire and Laboulbène, 1856, p. 373; Kraatz, 1868, p. 35; Redtenbacher, 1858, p. 119; Thomson, 1860, p. 298; Redtenbacher, 1874, p. 130; Fowler, 1888, p. 148; Ganglbauer, 1895, p. 255; Everts, 1898, p. 231; 1903, p. 103; Johansen, 1914, p. 241; Porta, 1926, p. 150; Rapp, 1933, p. 403.

Biology: Fauconnet, 1887, p. 91; Xamheu, 1902, pp. 1–53; 1903, pp. 178–180; 1910, p. 21; Rapp, 1933, p. 404.

*Diagnosis.* No other genus of Falagriini occurring in America north of Mexico can be confused with *Cordalia*. Distinguishing characters of adults, besides the characteristic habitus (Fig. 1), are the globose, cordiform prothorax; the presence of a depression at the base of the elytra near the humerus; and the mesocoxal acetabula margined posteriorly by a fine ridge (Fig. 76).

*Description.* Head about as broad as prothorax, arcuate-truncate at base, basal angles broadly rounded, vertex impressed at middle in male. Neck nearly  $\frac{1}{3}$  as wide as head including eyes. Eyes small. Labrum (Fig. 23A) transverse, slightly rounded at apex. Mandibles (Fig. 23D, E) moderate in size, slightly curved towards apex; right mandible with small obtuse tooth at middle of inner margin, finely crenulate between tooth and apex; left mandible simple, untoothed. Maxilla (Fig. 23C) with galea shorter than lacinia, pubescent on membranous apex; lacinia slightly curved towards tip, with a few spines between apex and middle of inner margin, pubescent below spines. Maxillary palpus (Fig. 23C) with segment 3 much longer and broader than 2; segment 4 long, cylindrical, truncate at apex, subuliform. Ligula (Fig. 23B) bifid to middle, lobes rounded at apex. Labial palpus (Fig. 23B) with segment 1 long and broad; segment 2 much shorter and narrower than 1; segment 3 longer than 2, feebly conical, truncate at apex. Antenna moderately long, broadened towards apex; segments 1–3 nearly subequal in length; segment 4 very slightly transverse; segments 5–10 gradually more transverse; segment 11 shorter than 9 and 10 combined. Prothorax (Fig. 32) globose, cordiform, strongly narrowed posteriorly, much narrower than elytra at greatest width, finely (or obsoletely) sulcate along median line, sulcus without ante-basal impression. Mesospiracular peritremes within prosternal membrane large, quadrate, contiguous along median line. Mesosternal process very short, not quite extending to anterior  $\frac{1}{4}$  of mesocoxae, broad and truncate apically. Metasternal process longer than mesosternal process, flat, transversely truncate at apex, separated from mesosternal process by short, flat isthmus. Mesocoxae broadly separated; acetabula margined behind by fine ridge. Hypomera not delimited from disc by marginal ridge. Scutellum flat, moderately punctured and pubescent. Elytra moderate in size, longer than prothorax along sutural line, each with a distinct depression at base near humerus. Abdomen elongate, broad, at base scarcely narrower than elytral apex. Terga III–V transversely impressed at base.

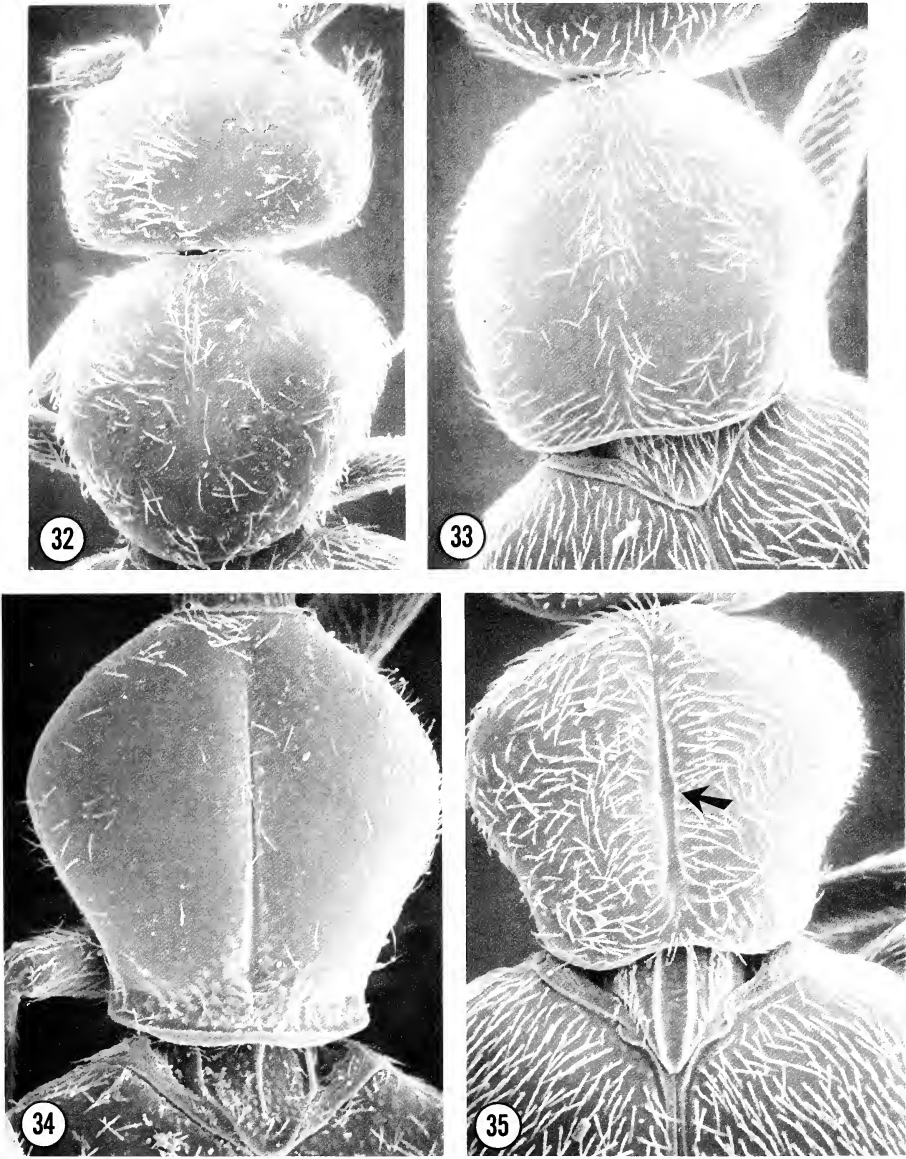
Members of the genus *Cordalia* are distributed throughout much of the world, but with greatest species diversity in the Ethiopian region. A single species, *obscura* (Grav.), occurs in America north of Mexico.

*Cordalia obscura* (Gravenhorst)

Figs. 1, 23, 32, 51, 70, 76, 81, 102; Map 1

*Aleochara obscura* Gravenhorst, 1802, p. 74 [type locality, Brunsvigae]; 1806, p. 151; Gyllenhal, 1810, p. 379; Sahlberg, 1834, p. 346.





Figs. 32–35. Prothoraces of North American Falagriini, dorsal aspect. 32. *Cordalia obscura*. 33. *Falagriota occidua*. 34. *Myrmecocephalus cingulatus*. 35. *Falagria dissecta* (arrow indicates small pocket-like depression near middle of sulcus).



*Cardiola obscura*; Mulsant and Rey, 1875, p. 455; Reitter, 1909, p. 75; Portevin, 1929, p. 294.

*Falagria obscura*; Mannerheim, 1831, p. 87; Boisduval and Lacordaire, 1836, p. 556; Erichson, 1839, p. 295; 1840, p. 54; Heer, 1839, p. 351; Redtenbacher, 1849, p. 651; Fairmaire and Laboulbène, 1856, p. 373; Kraatz, 1856, p. 35; Redtenbacher, 1858, p. 119; Thomson, 1860, p. 298; Redtenbacher, 1874, p. 130; Fowler, 1888, p. 148; Ganglbauer, 1895, p. 255; Everts, 1898, p. 231; 1903, p. 103; Johansen, 1914, p. 241; Porta, 1926, p. 150; Rapp, 1933, p. 403.

*Cordalia obscura*; Jacobs, 1925, p. 82; Scheerpeltz, 1930, p. 73; Scheerpeltz, 1934, p. 1568; Cameron, 1939, p. 236; Tottenham, 1949, p. 387; Horion, 1951, p. 168; Hansen, 1954, p. 100; Horion, 1967, p. 199; Arnett, 1968, p. 288; Palm, 1968, p. 78; Moore and Legner, 1975, p. 390.

*Falagria flavipes* Stephens, 1832, p. 105 [type locality, Great Britain, Bristol].

*Falagria floralis* Stephens, 1832, p. 105 [type locality, Great Britain, Norfolk].

*Aleochara immunis* Stephens, 1832, p. 129 [type locality, Great Britain].

*Falagria nitens* Stephens, 1832, p. 105 [type locality, Great Britain, London].

*Falagria crassiuscula* Hochhuth, 1871, p. 87 [type locality, Russia].

*Diagnosis.* Characters of the genus.

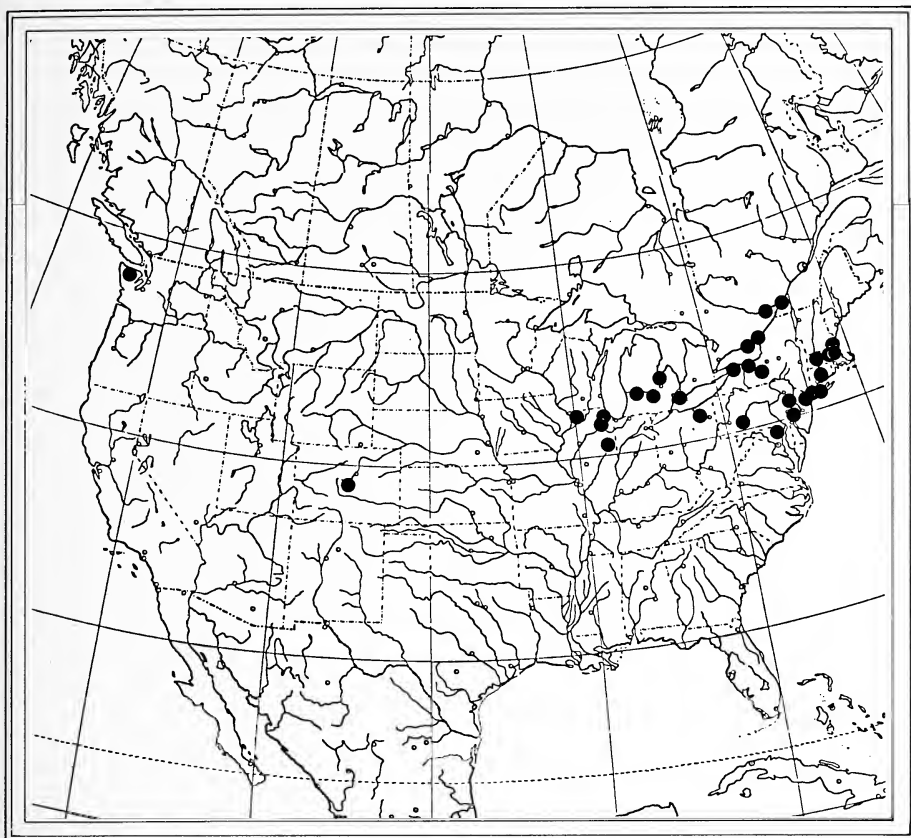
*Description.* Length 2.0–2.8 mm ( $N = 64$ ,  $\bar{x} = 2.44$  mm). Body stout, convex. Color dark rufo-testaceous; head, prothorax and abdomen behind segment II usually darker than elytra; mouthparts, antennae and legs pale. Habitus as in Figure 1.

Head (Fig. 32) small, arcuate-truncate at base, vertex impressed in front of occiput (in male only), slightly longer than wide, sides parallel. Surface minutely, sparsely punctured; pubescence moderate to dense; surface between punctures smooth and polished. Eyes slightly shorter than temples. Antenna moderately long, extending to middle of elytra. Prothorax (Fig. 32) cordiform, very convex dorsally, slightly wider than head, sides arcuate, strongly converging to base. Disc slightly sulcate along median line. Surface minutely, sparsely punctured and pubescent; surface between punctures smooth and shining. Elytra with surface finely, densely punctured and pubescent; surface between punctures smooth and shining. Abdomen broad at base, slightly narrower than elytra. Terga III–V broadly and transversely impressed at base; impressions coarsely punctured (Fig. 51). Tergal surfaces densely punctured; surface between punctures smooth and polished.

*Male.* Eighth tergite with apical margin broadly emarginate at middle, densely fimbriate (Fig. 70). Apical margin of sternum VIII broadly, evenly rounded. Median lobe of aedeagus as in Figure 81A. Paramere as in Figure 81B.

*Female.* Eighth tergite and sternite with apical margin as in male. Spermatheca as in Figure 102.

*Type material.* *Aleochara obscura* Gravenhorst. Lectotype, here designated, with the following labels: "Europa, Hist. Coll. Nr. 5296"/TYPUS/Zool. Mus. Berlin; my lectotype designation label is attached to it. In addition, I have examined 3 paralectotypes labeled the same as the lectotype, 2 with labels: Hist. Coll. Nr. 5296/Typus/Zool. Mus. Berlin, and 1 with labels: "5296"/Typus/obscura Gr./Zool. Mus. Berlin. All specimens are in the Gravenhorst collection of the Institut für Spezielle Zoologie und Zoologische Museum, Humboldt Universität, Berlin.



Map 1. Distribution of *Cordalia obscura*.

Type specimens of the Stephens and Hochhuth species, described from Great Britain and Russia, respectively, have not been examined.

**Distribution.** *Cordalia obscura* is widely distributed in northeastern United States and eastern Canada, but also is known from localities in Colorado and Washington (Map 1). Specimens have been collected from March through December.

**Material examined.** 418 specimens. CANADA: *Ontario*: Ottawa, April, June (CNCI) 2; Ottawa, June (CNCI) 1; Prince Edwards Co., March (CNCI) 1; Kent Co., Tilbury, June, October (FMNH) 2; Gananoque, May (CNCI) 5. *Quebec*: Montreal, September (CNCI) 7; Hudson Heights, August (CNCI) 1. UNITED STATES: *Colorado*: Deer Creek Canyon, July (CASC) 3. *Connecticut*: Stony Creek, May (CNCI) 1. *Illinois*: Urbana, Champaign Co., July (INHS) 13; Rogers Park, April (AMNH) 1; Glen View, September (FMNH) 5; Tiedtville, September (FMNH) 2; Cook Co., Hazelcrest, September (FMNH) 26; Cook Co., Homewood, September (FMNH) 1; Cook Co.,

Homewood, May, September, October (FMNH) 125; Cook Co., Chicago, July (FMNH) 1; JoDavies Co., 9 mi. S. of Stockton, October (FMNH) 48; Raccoon Grove, 2 mi. S. of Monee, Will Co., October (FMNH) 1; Chicago, July, October, November (ZMB) 13; Beverly Hills, Chicago, June (ZMB) 8. *Maryland*: Baltimore (FMNH) 1. *Massachusetts*: Northampton, June, August, September (CNCI) 4; Arlington, January, March, April (MCZC) 4; Cambridge, March (MCZC) 1; Framingham, October (MCZC) 1; Berlin, June (CUIC) 1; Needham, September (CASC) 10; Ashland, November (MCZC) 1. *Michigan*: Kent Co., Grand Rapids, July, August (ERHC) 26; Bath, March (MSUC) 1; Midland Co., June (MSUC) 1. *New Hampshire*: Rockingham Co., Odiornes Pt. St. Pk., June (DENH) 1. *New Jersey*: Berkeley Heights, May (AMNH) 2; Avenel (AMNH) 1; Bergen Co., Waldwick, August (JHFC) 8. *New York*: Ithaca, May (MCZC) 1; Ithaca, April, August, September, October (CUIC, FMNH) 165; Romulus, April, May (ERHC) 4; Flatbush, Long Island, November (CUIC, FMNH) 6; Brooklyn, March, May (CUIC, AMNH) 2; Olcott, April (CUIC) 1; Staten Island, March, December (AMNH, FMNY) 5; Queens (FMNH) 1; Rochester, August (AMNH) 2; McLean Bogs Reserve, May (ZMB) 1. *Pennsylvania*: Angora, June (MCZC) 1; Easton, March, April, May, June, July, August (CASC, MCZC) 41; Jeannette, October, November (AMNH) 5. *Ohio*: Summit Co., August (INHS) 1. *Washington*: Lake Sutherland, August (CUIC) 1.

*Habitat*. Horion (1967:199) claimed this species is common in decaying plant material and also in carrion and dung. Hicks (1959) has recorded *C. obscura* from nests of several bird species, including woodpecker, jackdaw, and hoopoe. In America north of Mexico this species has been taken by sifting grass clippings, from a berlese sample of decaying vegetation and compost, from a rotting bracket fungus, from garden soil, and from a bacon bait trap.

## 2. *Falagriota* Casey

*Falagriota* Casey, 1906, p. 255; Fenyes, 1912, pp. 20, 22, 26; 1918, p. 18; 1920, p. 156; Leng, 1920, p. 124; Notman, 1920, p. 731; Bernhauer and Scheerpeltz, 1926, p. 573; Bradley, 1930, p. 85; Scheerpeltz, 1934, p. 1569; Blackwelder, 1952, p. 165; Arnett, 1968, p. 289; Seevers, 1978, p. 147.

*Type-species*: *Falagria occidua* Casey, fixed by subsequent designation (Fenyes, 1912, p. 22).

*Diagnosis*. Distinguishing characters of adults are the faintly sulcate pronotum, lack of a comb of denticles on the apical margin of tergum VIII, simple and unmodified scutellum, delimited hypomera, uniform punctation of the elytra, and reduced mesothoracic peritremes (Fig. 77).

*Description*. Head moderate in size, rounded at base; surface very slightly impressed along median line towards base. Neck narrow, about  $\frac{1}{4}$  as broad as head across eyes. Eyes moderate in size, not prominent. Labrum (Fig. 24A) rounded on sides and front margin. Mandibles (Fig. 24D, E) rather short, stout; right mandible with robust tooth at middle of inner margin; left mandible simple. Maxilla (Fig. 24C) with galea almost as long as lacinia, finely pubescent on membranous apex; lacinia curved towards hooked apex, with a few elongate, curved and stout spines between middle of inner margin and apex, densely pubescent below spines. Maxillary palpus (Fig. 24C) rather

elongate; segment 3 longer, very slightly wider than 2; segment 4 long, subuliform. Mentum transversely trapezoidal, truncate in front. Ligula (Fig. 24B) narrow, bifid to about middle. Labial palpus (Fig. 24B) with segment 1 long and broad; segment 2 much shorter and narrower than 1; segment 3 much longer and narrower than 2, nearly cylindrical, subtruncate at apex. Antenna rather long, gradually broadened distally; segments 1–3 subequal in length; segments 4–10 slightly transverse; segment 11 as long as 9 and 10 combined. Prothorax moderately narrowed towards base. Disc finely sulcate, faintly and inconspicuously impressed along median line. Prosternum moderately large, hind margin broadly and obtusely angulate, acutely cusped at middle. Mesospiracular peritremes small, triangular, transverse and broadly separated along median line, membrane broadly exposed. Mesosternal process extending to middle of mesocoxal cavities, narrowed towards subtruncate apex. Metasternal process short, separated from mesosternal process by a long, transversely and strongly convex, depressed isthmus. Mesocoxae narrowly separated. Hypomera clearly delimited from disc by marginal ridge. Scutellum simple, flat, coarsely punctured and pubescent. Elytra slightly longer or, in some specimens, shorter than pronotum, evenly convex; lateral margins nearly straight and subparallel, posterior margins sinuate at outer angles. Abdomen broad at base, nearly as broad as elytra. Terga III–V transversely and broadly impressed at base; impressions moderately, but not densely, coarsely punctate. Apical margin of tergum VIII simple, without fine denticles or fimbriate edge.

The genus *Falagriota* is represented in America north of Mexico by a single species, *occidua* (Casey).

*Falagriota occidua* (Casey)

Figs. 2, 24, 33, 52, 77, 78, 82, 103; Map 2

*Falagria occidua* Casey, 1885, p. 285 [type locality, California, Santa Clara Co., Gilroy Hot Springs].

*Falagriota occidua*; Casey, 1906, p. 256; Fenyés, 1920, p. 156; Bernhauer and Scheerpeltz, 1926, p. 573; Bradley, 1930, p. 85; Seevers, 1978, p. 147.

*Falagriota lucida* Casey, 1906, p. 257 [type locality, California, Monterey Co., Paraiso Hot Springs].

*Falagriota asperula* Casey, 1906, p. 257 [type locality, California, Los Angeles Co., Pomona Mts.].

*Falagriota picina* Casey, 1906, p. 257 [type locality, California, Los Angeles Co., Pomona Mts.].

*Falagriota evanescens* Casey, 1906, p. 258 [type locality, California, Sonoma Co.].

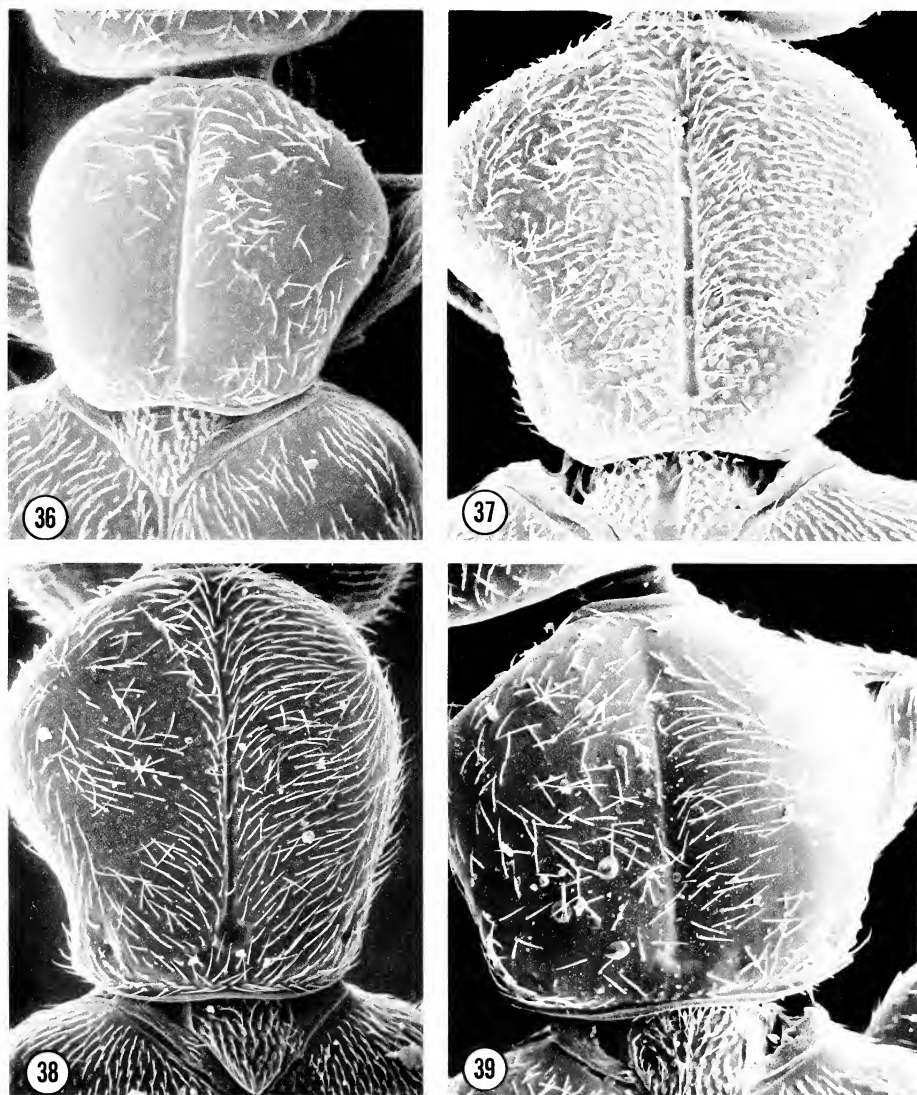
*Falagriota collaris* Casey, 1906, p. 258 [type locality, California, Humboldt Co., Hoopa Valley].

*Falagriota parvipennis* Casey, 1906, p. 259 [type locality, California, San Bernardino Mts.].

*Diagnosis.* Characters of the genus.

*Description.* Length 2.1–2.8 mm ( $N = 42$ ;  $\bar{x} = 2.46$  mm). Color rufo-testaceous to rufo-piceous; mouthparts, basal antennal segments and legs usually paler. Habitus as in Figure 2.





Figs. 36–39. Prothoraces of North American Falagriini, dorsal aspect. 36. *Leptagria pexilis*. 37. *Aleodorus scutellaris*. 38. *Lissagria laticeps*. 39. *Borboropora quadriceps*.

Head slightly wider than long, broadly rounded at base. Surface sparsely and very finely punctured and pubescent; surface between punctures smooth and shining. Eyes nearly equal to length of temples. Antenna relatively long, reaching basal third of elytra. Prothorax (Fig. 33) elongate, longer than but equal to width of head, gradually narrowed behind and distinctly converging to base. Disc obsoletely sulcate along



median line; transverse subbasal impression present but indistinct. Surface very finely and moderately densely punctured and pubescent; surface between punctures smooth and shining. Scutellum (Fig. 33) simple, flat, coarsely punctured and pubescent. Elytra with surface uniformly, sparsely and finely punctured and pubescent; surface between punctures smooth and polished. Abdomen (Fig. 52) broad at base, not quite as broad as elytra. Terga III–V transversely, shallowly impressed at base; impressions with few to numerous coarse, but separated punctures. Tergal surfaces sparsely, finely punctured and pubescent; surface between punctures smooth and shining.

*Male.* Eighth tergite with apical margin truncate, simple. Eighth sternite with apical margin broadly, evenly rounded. Median lobe of aedeagus as in Figure 82A. Paramere as in Figure 82B.

*Female.* Eighth tergite and sternite with apical margin as in male. Spermatheca as in Figure 103.

*Type material.* *Falagria occidua* Casey. Lectotype, here designated, with the following labels: "Cal" [=Gilroy Hot Springs, Santa Clara Co.]/CASEY bequest 1925/Type USNM 38939/"occidua Cas."; my lectotype designation label is attached to it. Seven paralectotypes have labels identical to those of the lectotype, while four paralectotypes have the labels: "Cal" [=Paraiso Hot Springs, Monterey Co.].

*Falagriota lucida* Casey. Holotype, with the following labels: "Cal" [=Paraiso Hot Springs, Monterey Co.]/CASEY bequest 1925/Type USNM 38940/"lucida Csy."/CASEY determ occidua-10.

*Falagriota asperula* Casey. Holotype, with labels as follows: "Pom Mts., Cal., Sep"/CASEY bequest 1925/Type USNM 38937/"asperula Csy."

*Falagriota picina* Casey. Holotype, with the labels: "Pom Mts., Cal., Sep"/CASEY bequest 1925/Type USNM 38937/"picina Csy."

*Falagriota evanescens* Casey. Holotype, with the following labels: "Sonoma Co., Cal. "/CASEY bequest 1925/Type USNM 38938/"evanescens Csy."

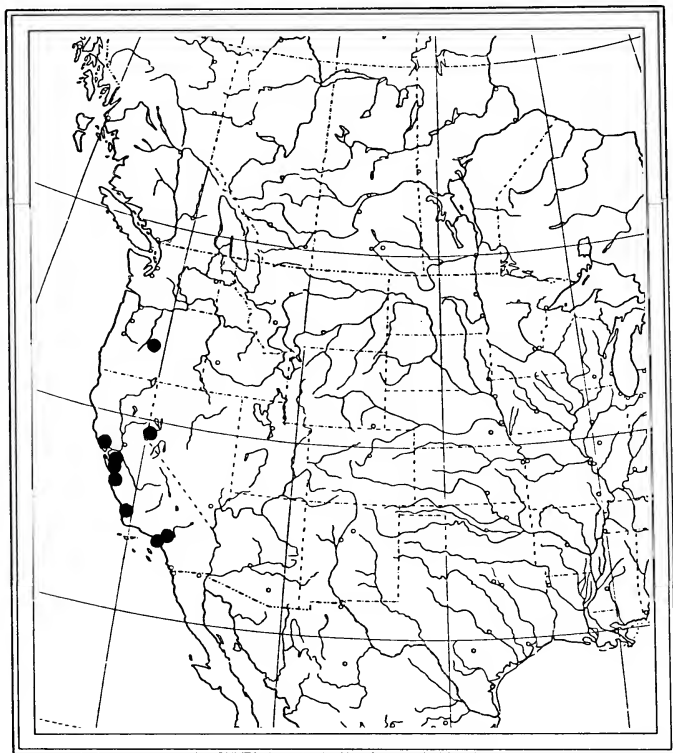
*Falagriota parvipennis* Casey. Holotype, with labels as follows: "Mts. S.B., 7.17.92, Cal. "/CASEY bequest 1925/Type USNM 38934/"Falagriota parvipennis Csy."

*Falagriota collaris* Casey. Lectotype, here designated, with the following labels: "Cal" [Hoopa Valley, Trinity River, Humboldt Co. (Fort Gaston).]/CASEY bequest 1925/Type USNM 38935/"collaris Csy."; my lectotype designation label is attached to it. One other paralectotype is labeled as the lectotype.

Type specimens of the above 7 nominal species are in the Casey collection of the U.S. National Museum (Natural History), Washington.

*Distribution.* *Falagriota occidua* at present is known only from California, Oregon and Nevada (Map 2). Specimens have been collected from February through December.

*Material examined.* 102 specimens. UNITED STATES: *California*: Pasadena, September, October (MCZC, CASC, AMNH) 8; Los Angeles (MCZC, USNM) 2; Carson (USNM) 7; San Dimas Canyon, San Gabriel Mts., Los Angeles Co., July, August, (INHS) 19; Carmel, July (MCZC) 1; San Bernadino Mts., July (MCZC) 3; Alameda Co., May (USNM) 1; Piedmont, June (AMNH) 1; Oakland, Alameda Co., February (UCBC) 2; Sonoma (USNM) 5; Los Gatos (USNM) 4; Baywood Park, September (CNCI) 1; Baywood Park, San Luis Obispo Co., December (UCRC) 1; Poly Canyon, San Luis Obispo Co., October (CNCI) 2; Mill Valley, Marin Co., October (CASC)



Map 2. Distribution of *Falagriota occidua*.

6; Alhambra, Contra Costa Co., July (CASC) 1; Mt. Diablo, Contra Costa Co., February (UCBC) 1; Perkins Gulch, 7 mi SE of Clayton, Contra Costa Co., July (UCBC) 1; Santa Cruz Co., 14 mi N of Boulder Creek, 2,630 ft, October (AMNH) 11; Pom. Mts., May, September (MCZC) 5; Pomona, September (MCZC) 1; Panamint Mts., April (CASC) 8; San Mateo, February (CUIC) 2; state label only (USNM) 1. *Nevada*: Carson City, July (MCZC) 7. *Oregon*: State label only (MCZC) 1.

*Habitat*. Little is known about the habitat of this species. Specimens at hand have been collected by sifting debris under dead leaves, and from manzanita (*Arctostaphylos* sp., Ericaceae) duff in California.

### 3. *Myrmecocephalus* MacLeay

*Myrmecocephalus* MacLeay, 1873, p. 134.

As subgenus of *Falagria*: Tottenham, 1957, p. 90; Blackwelder, 1952, p. 253; Arnett, 1968, p. 289; Moore and Legner, 1975, p. 414.

As synonym of *Stenagria*: Bernhauer and Scheerpeltz, 1926, p. 575.

*Type-species*: *Myrmecocephalus cingulatus* MacLeay, fixed by subsequent designation (Blackwelder, 1952, p. 253) (= *australica* Bernhauer and Scheerpeltz (1926), new name).

*Stiliciodes* Broun, 1880, p. 95.

As synonym of *Stenagria*: Bernhauer and Scheerpeltz, 1926, p. 575; Blackwelder, 1952, p. 362.

*Type-species*: *Stiliciodes micans* Broun, fixed by monotypy (Broun, 1880, p. 95).

*Stenagria* Sharp, 1883, p. 237; Fenyes, 1912, pp. 20, 23; 1918, p. 18; 1920, p. 159; Notman, 1920, p. 731; SeEVERS, 1978, p. 146.

As subgenus of *Falagria*: Bernhauer and Scheerpeltz, 1926, pp. 575, 576; Scheerpeltz, 1934, p. 1572; Last, 1979, p. 233.

As synonym of *Myrmecocephalus*: Blackwelder, 1952, p. 358; Tottenham, 1957, p. 90.

*Type-species*: *Stenagria gracilipes* Sharp, fixed by subsequent designation (Fenyes, 1912, p. 23).

*Lorinota* Casey, 1906, p. 238; Fenyes, 1912, pp. 21, 23, 27; 1918, p. 18; 1920, p. 158; Notman, 1920, p. 731.

As synonym of *Stenagria*: Bernhauer and Scheerpeltz, 1926, p. 575; Scheerpeltz, 1934, p. 1572; SeEVERS, 1978, p. 146.

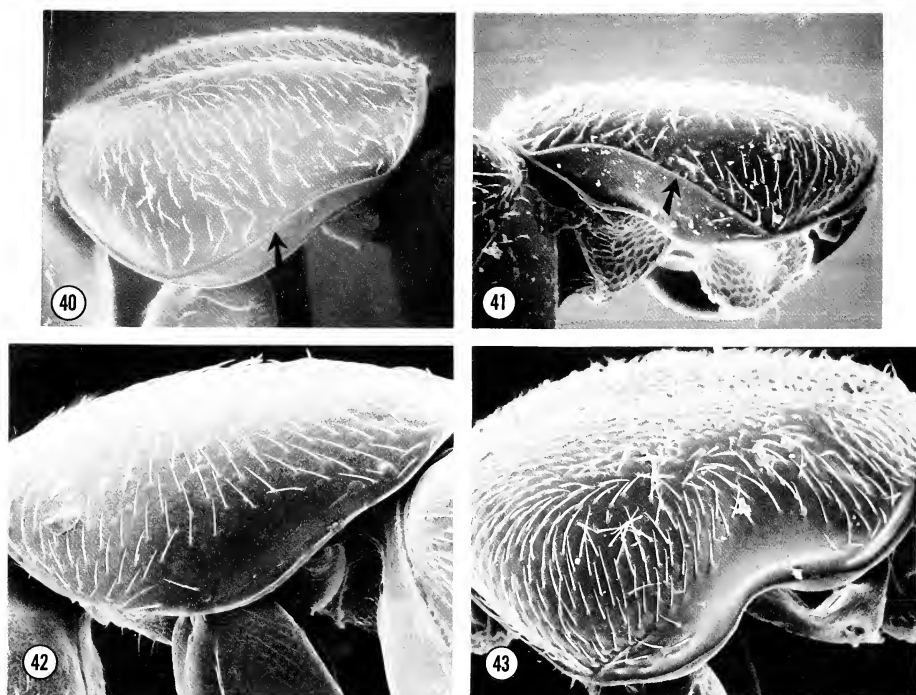
As synonym of *Myrmecocephalus*: Blackwelder, 1952, p. 227.

*Type-species*: *Falagria cingulata* LeConte, fixed by subsequent designation (Fenyes, 1912, p. 23).

Biology: Rupertsberger, 1880, p. 115; Ganglbauer, 1895, p. 254; Xamheu, 1910, p. 20.

*Diagnosis*. Distinguishing adult characters are the absence of a comb of denticles on the apical margin of tergum VIII (Fig. 71), unicarinate scutellum (complete or incomplete) (Fig. 34), delimited hypomera (Fig. 40), long, slender legs, and characteristic habitus (Figs. 3–10).

*Description*. Head rounded or arcuate-truncate at base, at least as broad as prothorax. Neck very narrow. Eyes moderately large, prominent. Labrum (Fig. 25A) transverse, strongly rounded at sides, subtruncate along frontal margin. Mandibles (Fig. 25D, E) moderate in size, curved towards acute apex; right mandible with a rather obtuse tooth at middle of inner margin; left mandible simple. Maxillae (Fig. 25C) with galea shorter than lacinia, pubescent on membranous apex; lacinia hooked at apex, with 4 or 5 rather long spines between apex and middle of inner margin, finely setose below spines. Maxillary palpus (Fig. 25C) slender, elongate; segment 3 longer, but not wider than 2; segment 4 long, subulate. Mentum (Fig. 25B) strongly transverse, narrowed in front, slightly emarginate on front margin. Ligula (Fig. 25B) deeply bifid almost to base, lobes rounded at apex. Labial palpus (Fig. 25B) with segment 1 long and broad; segment 2 much shorter and narrower than 1; segment 3 longer than 2, obconical, truncate at apex. Antenna moderately long; segments 1–3 subequal in length, elongate; segment 11 almost as long as 9 and 10 combined. Prothorax elongate, convex, very strongly narrowed towards base. Disc deeply sulcate along median line. Prosternum moderately large before front coxae, posterior margin finely cusped at middle. Mesospiracular peritremes large, quadrate, contiguous along median line. Mesosternal process projecting between mesocoxae to about anterior  $\frac{1}{3}$  to  $\frac{1}{2}$ , parallel-sided, rounded and free at apex, separated from metasternal process by a short, somewhat depressed isthmus. Mesocoxae moderately separated. Hypomera long and narrow, delimited from pronotal disc by marginal ridge. Scutellum



Figs. 40–43. Prothoraces of North American Falagriini, lateral aspect. 40. *Myrmecocephalus pinalicus*. 41. *Falagrioma thoracica*. 42. *Lissagria laeviuscula*. 43. *Aleodorus scutellaris*. (Arrows indicate marginal ridge delimiting hypomera from pronotal disc.)

densely punctured, finely carinate along median line (Fig. 34), carina incomplete in some specimens of some species (distinct at base only). Elytra much broader than prothorax, longer than broad; parallel-sided or slightly arcuate posteriorly along lateral margins; posterior margins sinuate at outer angles. Surface evenly convex, finely and uniformly punctured and pubescent, with or without fine surface microsculpture. Abdomen elongate, parallel-sided. Terga III–V transversely impressed at base; impressions punctured or impunctate. Tergal surfaces smooth, with or without fine microsculpture; finely, sparsely or densely punctured and pubescent. Apical margin of tergum VIII simple.

The genus *Myrmecocephalus* is found in all major zoogeographic regions. Eight species occur in America north of Mexico, including two described as new in this paper (*gatineauensis* and *sculpturatus*).

*Remarks.* There has been confusion regarding the correct name to apply to this generic concept. The genera *Lorinota* Casey and *Stenagria* Sharp were first listed as synonyms of *Myrmecocephalus* MacLeay, an Australian genus, by Blackwelder (1952). Seevers (1978), however, remained unconvinced of this decision, stating that “these synonymies require confirmation,” and instead recognized the genus *Stenagria*, based on a Central American species. I have examined specimens of the type species of all



genera in question and conclude that all are congeneric. Adherence to priority of publication makes the generic name *Myrmecocephalus* MacLeay valid.

#### KEY TO SPECIES OF *Myrmecocephalus*

1. Small, usually less than 3.0 mm; abdomen bicolored (basal 2 segments generally light in color, apical segments dark) (Figs. 3–5) ..... 2
- Larger, usually greater than 3.0 mm; abdomen unicolorous ..... 4
2. Head broadly rounded at base (Fig. 3); impression of tergum III coarsely and rugosely sculptured (Fig. 53) ..... *cingulatus* (LeConte)
- Head distinctly arcuate-truncate at base (Fig. 4); impression of tergum III not as above ..... 3
3. Impression of tergum III impunctate, smooth and polished, or nearly so (Fig. 54); posterior angles of pronotum slightly produced as a small projection; spermatheca as in Figure 105 ..... *concinus* (Erichson)
- Impression of tergum III usually coarsely punctate at the middle; posterior angles of pronotum not produced; spermatheca as in Figure 106 ..... *gracilis* (Casey)
4. Dorsal surface of head, pronotum and elytra with reticulate microsculpture (Fig. 64) ..... *sculpturatus* sp. nov.
- Dorsal body surfaces without reticulate microsculpture; microsculpture, when present, consisting of transverse wavy microlines (Figs. 67–69) ..... 5
5. Abdominal terga with microsculpture ..... 6
- Abdominal terga without microsculpture, smooth and polished (Fig. 66) ..... *arizonicus* (Casey)
6. Abdominal terga very minutely and sparsely punctured throughout; surface slightly sculptured with transverse wavy microlines (Figs. 68, 69) ..... 7
- Abdominal terga finely and closely punctured throughout; surface densely sculptured with a fine network of transverse microlines (Fig. 67) ..... *gatineauensis* sp. nov.
7. Elytral surface with distinct microsculpture of transverse microlines (similar to that in Fig. 68); impression of tergum III usually impunctate ..... *caviceps* (Casey)
- Elytral surface without microsculpture; impression of tergum III generally coarsely punctured ..... *pinalicus* (Casey)

#### *Myrmecocephalus cingulatus* (LeConte)

Figs. 3, 25, 34, 53, 83, 104; Map 3

*Falagria cingulata* LeConte, 1866, p. 370 [type locality, New York].

*Myrmecocephalus cingulata*; Moore and Legner, 1975, p. 415.

*Lorinota tenuicornis* Casey, 1906, p. 243 [type locality, Iowa, Iowa City].

*Lorinota sinuosa* Casey, 1911, p. 178 [type locality, Wisconsin, Bayfield].

**Diagnosis.** Adults of *Myrmecocephalus cingulatus* are very similar to those of *M. concinns* and *gracilis* in size and color pattern, but are easily distinguished by the broadly rounded head (Fig. 3), and the coarsely and rugosely punctured basal impression of tergum III (Fig. 53).

**Description.** Length 2.3–3.3 mm (N = 91;  $\bar{x}$  = 2.68 mm). Color pale rufocastaneous; elytra paler at base in some specimens; apical four abdominal segments dark. Habitus as in Figure 3.

Head (Fig. 3) orbicular, convex, longer than broad, broadly and evenly rounded at base. Surface sparsely and minutely punctured and pubescent; surface between



punctures smooth and shining. Eyes slightly shorter than length of temples. Antenna long, reaching apical third of elytra. Prothorax (Figs. 3, 34) narrow and elongate, cylindrical, convex, distinctly narrower than head, broadest across anterior third, strongly converging to base; hind margins distinctly but narrowly reflexed. Disc deeply sulcate along median line except at extreme apex, sulcus ending in a small, deep, subbasal fovea. Surface strongly, evenly convex, sparsely and minutely punctured and pubescent; punctures more dense and asperate towards sulcus; surface between punctures smooth and shining. Scutellum finely carinate (Fig. 34), carina sometimes extending to apex but usually confined to base; surface sparsely, finely punctured and pubescent. Elytra with surface moderately, sparsely and minutely punctured; surface between punctures smooth and shining. Abdomen (Fig. 53) narrowed at base, parallel-sided. Terga III–V strongly and transversely impressed at base; tergum III narrow at base and more dilated caudad; impression of tergum III coarsely and rugosely punctured (Fig. 53); impressions of terga IV and V narrow, coarsely punctate at middle. Tergal surfaces very minutely and densely punctured and pubescent; surface between punctures very finely but distinctly sculptured with fine transverse micro-lines.

*Male.* Eighth tergite with apical margin truncate, simple. Apical margin of eighth sternite broadly rounded. Median lobe of aedeagus as in Fig. 83A. Paramere as in Figure 83B.

*Female.* Eighth tergite and sternite with apical margin as in male. Spermatheca as in Figure 104.

*Type material.* *Falagria cingulata* LeConte. Lectotype, here designated, with labels as follows: yellow disc [=Central Valley or Western States]/Type 6239/"F. cingulata LeC."; my lectotype designation label is attached to it. In addition, I examined five paralectotypes with labels as follows: yellow disc/"cingulata 2"; pink disc [=Middle States]/"cingulata 3"; "Penn.)/"cingulata 4"; "Ill.)/"cingulata 5"; and "Stone Cr., Lee Co., Va.)/113/"cingulata 6." All specimens are in the LeConte collection of the Museum of Comparative Zoology, Harvard University, Cambridge.

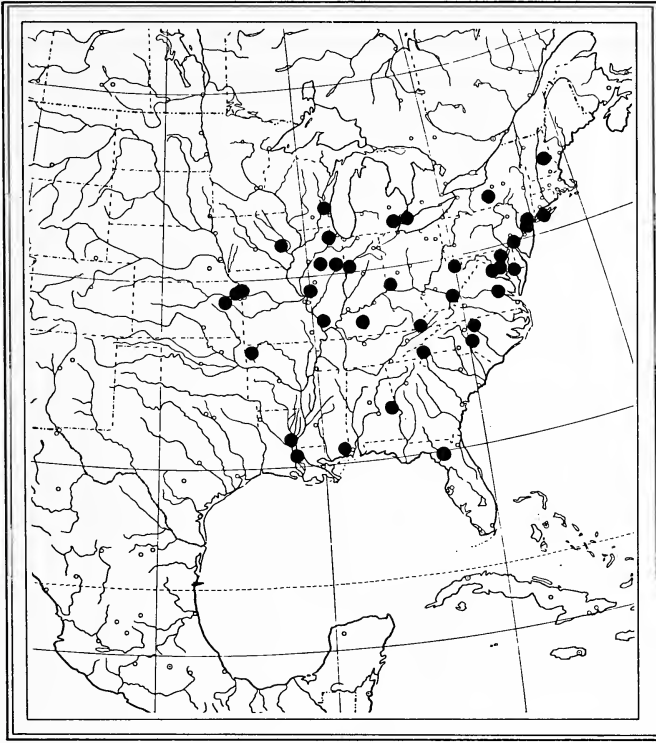
*Lorinota tenuicornis* Casey. Lectotype, here designated, with the following labels: "Iowa City, Iowa"/CASEY bequest 1925/Type USNM 38916/"tenuicornis Csy."; my lectotype designation label is attached to it. In addition, I also examined two paralectotypes with the labels "Cin., O." and "Ia."

*Lorinota sinuosa* Casey. Holotype, with labels as follows: "Bayfld., Wis., Wickham"/CASEY bequest 1925/Type USNM 38915/"sinuosa Csy."

Type specimens for the above two species are in the Casey collection of the U.S. National Museum (Natural History), Washington.

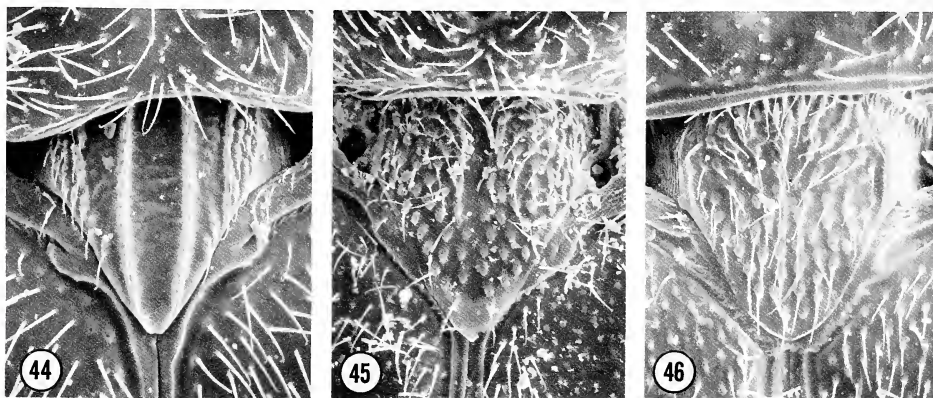
*Distribution.* *Myrmecocephalus cingulatus* is widely distributed in eastern North America, from Nova Scotia and Ontario south to Louisiana and Alabama and west to eastern Kansas (Map 3). Specimens have been collected from March through December.

*Material examined.* 161 specimens. CANADA: *Nova Scotia*: Wentworth, Cumberland Co., May (CNCI) 1. *Ontario*: Kent Co., Tilbury, September (FMNH) 1. UNITED STATES: *Alabama*: Auburn, March, April (CNCI) 8; Opelika, March (CNCI) 2. *Arkansas*: Washington Co., March (INHS) 1. *District of Columbia*: Washington (USNM) 3. *Florida*: Alachua Co., 7 mi. SE Branford, Santa Fe River, May



Map 3. Distribution of *Myrmecocephalus cingulatus*.

(DENH) 1. *Illinois*: Gillespie, September (INHS) 1; Urbana, March (INHS) 1; Urbana, April, May, July, August, September (INHS, FMNH) 6; White Heath, March (INHS) 1; Aurora, September (FMNH) 1; Pine Hills Field Sta., Union Co., May (CNCI) 1; Kane Co., Forest Preserve on AH 30, 3 mi S of Lily Lake, November (FMNH) 1; McLean Co., nr. Bloomington, Funk's Grove, September (FINH) 6; state label only (MCZC) 1. *Indiana*: Parke Co., 4 mi W of Rockville (Hajji Hollow), June (FMNH) 2; Smith, August (FMNH) 1. *Iowa*: Iowa City (FMNH) 1; state label only, September (USNM) 1. *Kansas*: Leavenworth (USNM) 2; Topeka, November (USNM, MCZC) 7; state label only (INHS, USNM) 3. *Kentucky*: Edmonton Co., Mammoth Cave Nat'l. Pk., Bruce Hollow, August (FMNH) 1. *Louisiana*: Concordia Pa., 5 mi W of Ferriday, May (CNCI) 1; state label only (MCZC) 1. *Maryland*: Bladensburg, October (USNM) 3; Cabin John, May (USNM) 1; Oakland (USNM) 1; Dorchester Co., nr. Lloyds, July (USNM) 4; Baltimore, July (CASC) 8; Prince Georges Co., Patuxent Wildlife Refuge, June (DENH) 2. *Michigan*: Ann Arbor (USNM) 1; state label only (MCZC) 2. *Mississippi*: Lucedale, February, April (CUIC) 3. *Missouri*: Platte City, May (UNHS) 1. *New Hampshire*: state label only (MCZC) 1. *New Jersey*: Highlands (AMNH) 1; Jamesburg, September (FMNH) 1; Ft. Lee, April (USNM) 1. *New York*: Ithaca, November (CUIC) 1; Lottwood, Flatbush, L.I. (AMNH) 1; Long



Figs. 44-46. Scutella of North American Falagriini, dorsal aspect. 44. *Falagria dissecta*. 45. *Aleodorus intricatus*. 46. *Borboropora quadriceps*.

Island label only (USNM) 4. *North Carolina*: Black Mts., June, July, September (AMNH) 3; Lake Toxaway (AMNH) 1; West End, December (FMNH) 1; Highlands, June (MCZC) 1; Orange Co., March (CUIC) 1; state label only (INHS) 3. *Ohio*: Cincinnati (CUIC, MCZC) 4. *Pennsylvania*: Manyunk, October (CASC) 2; Chestnut Hill, July, August (MCZC) 4; Allegheny (ICCM) 2; West View, May (ICCM) 1; state label only (FMNH) 1. *Virginia*: E. Falls Church, September (USNM) 1; Stone Cr., Lee Co. (USNM) 5; Straight Cr., Lee Co. (USNM) 1; Falls Church, May (USNM) 2; Rosslyn (USNM) 1; Great Falls, August, September (USNM) 2; Fairfax Co., September (USNM) 1. *West Virginia*: Grafton (USNM) 6; White Sulphur Springs, July (FMNH) 1; state label only (USNM, MCZC) 24. *Wisconsin*: West Bend, Washington Co., August (CNCI) 1.

*Habitat*. Specimens at hand have been taken from under bark, from fungus on a stump, from a sawdust pile, and from various litter.

*Myrmecocephalus concinnus* (Erichson)

Figs. 4, 54, 84, 105; Map 4

*Falagria concinna* Erichson, 1840, p. 51 [type locality, Brasil].

*Myrmecocephalus concinna*; Nakane et al., 1963, p. 98.

*Falagria longipes* Wollaston, 1871, p. 284 [type locality, Madeira, western outskirts of Funchal].

*Falagria fovea* Sharp, 1874, p. 3 [type locality, Japan].

*Falagria parae* Sharp, 1876, p. 41 [type locality, Amazon Valley, Pará, Brasil].

*Falagria currax* Sharp, 1880, p. 37 [type locality, Hawaiian Islands].

*Lorinota bilimbata* Casey, 1906, p. 245 [type locality, Iowa, Iowa City]. **New Synonym.**

*Diagnosis*. Adults closely resemble those of *cingulatus* but are distinguishable by the arcuate-truncate head (Fig. 4), impunctate basal impression of abdominal tergum III in most specimens (Fig. 54), and projecting basal angles of the pronotum. Females

can be separated from those of *cingulatus* by the characteristically shaped spermatheca (Fig. 105), and notched apex of sternum VIII.

*Description.* Length 2.5–3.4 mm ( $N = 32$ ;  $\bar{x} = 2.74$  mm). Color light brownish to reddish yellow; intermediate antennal segments and center of elytra usually darker brown; terminal four abdominal segments dark brown to nearly piceous. Habitus as in Figure 4.

Head small, round, distinctly arcuate-truncate at base (Fig. 4). Surface densely and finely punctured and pubescent; surface between punctures smooth and polished. Eyes equal to length of temples. Antenna moderate in length, reaching to anterior third of elytra. Prothorax (Fig. 4) elongate-cylindrical, convex, slightly longer than head, broadest at anterior third, strongly converging to base; basal margin distinctly reflexed; basal angles acutely produced, projecting. Disc deeply sulcate along median line, except at extreme apex, sulcus ending in a shallow, round, subbasal fovea; transverse impression radiating from fovea on each side. Surface densely and very finely punctured and pubescent; surface between punctures smooth and shining. Scutellum finely carinate along median line, carina extending to or nearly to apex; surface coarsely and densely punctured and pubescent. Elytra with surface densely, uniformly and finely punctured and pubescent; surface between punctures smooth and shining. Abdomen (Fig. 54) narrowed at base, but nearly as broad at base as elytra. Terga III–V slightly impressed at base; basal impressions without punctures (Fig. 54), or with only few obsolete punctures. Tergal surfaces finely punctured and pubescent; surface between punctures indistinctly sculptured with fine transverse microlines.

*Male.* Eighth tergite with apical margin truncate, simple. Eighth sternite with apical margin broadly rounded. Median lobe of aedeagus as in Figure 84A. Paramere as in Figure 84B.

*Female.* Eighth tergite with apical margin as in male. Eighth sternite with apical margin deeply notched at middle. Spermatheca as in Figure 105.

*Type material.* *Falagria concinna* Erichson. Lectotype, here designated, with labels: "Brasil, Germ., Hist. Coll. Nr. 5288"/Typus/Zool. Mus. Berlin; my lectotype designation label is attached to it. In addition, I examined one other paralectotype with labels identical to the lectotype. One other paralectotype had the labels: 5288/Typus/"concinna Er., Bras., Gm.,"/Zool. Mus. Berlin, while two others were labeled: "Columb. Otto, Hist. Coll. Nr. 5288"/Typus/Zool. Mus. Berlin. All specimens are in the Erichson collection of the Institut für Spezielle Zoologie und Zoologische Museum, Humboldt-Universität, Berlin.

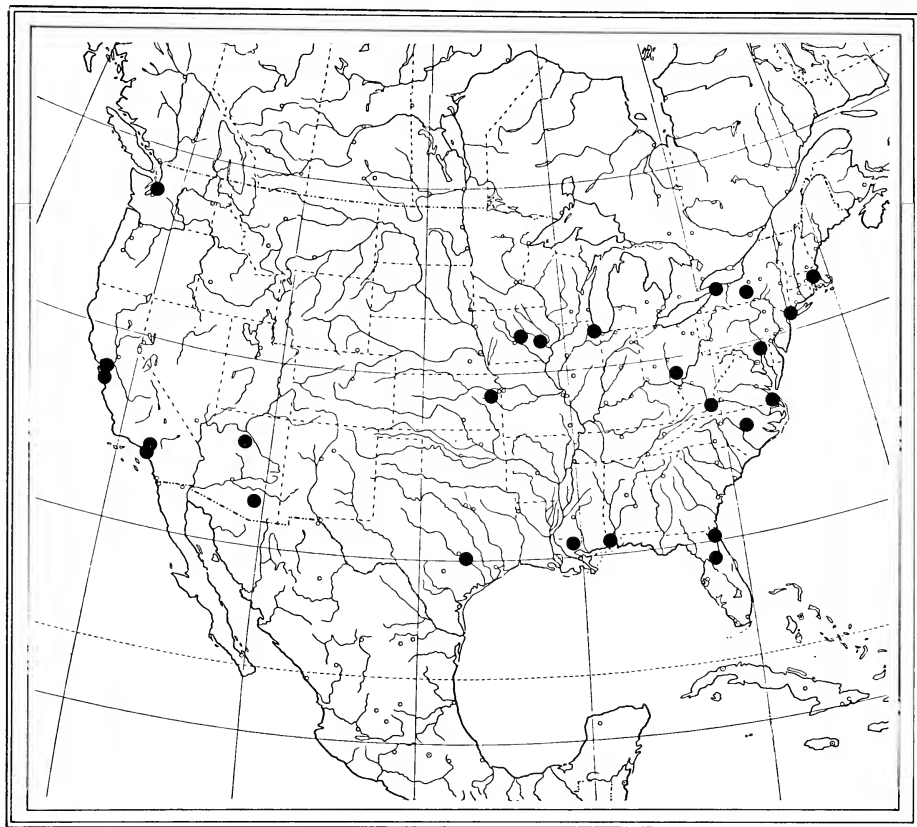
*Lorinota bilimbata* Casey. Lectotype, here designated, with the following labels: "Iowa City, Iowa"/CASEY bequest 1925/Type USNM 38919/"bilimbata Csy."; my lectotype designation label is attached to it. One paralectotype is labeled: "Ia.,"/ "paratype-2." Both specimens are in the Casey collection of the U.S. National Museum (Natural History), Washington.

Type specimens of the Sharp and Wollaston species were not examined.

*Distribution.* *Myrmecocephalus concinnus*, a cosmopolitan species, is transcontinental in North America (Map 4). Specimens have been collected from March through June, and during January, August, October and November.

*Synonymy.* The type specimens of *bilimbata* are indistinguishable from specimens





Map 4. Distribution of *M. concinnus*.

of *concinnus*. I could not find sufficient characters to separate the two. The characters given by Casey (1906) for *bilimbata* correspond to the same characters diagnostic for *concinnus*.

*Material examined.* 44 specimens. UNITED STATES. *Alabama*: Mobile (CASC) 3. *Arizona*: Flagstaff (FMNH) 1. *California*: Los Angeles, June (FMNH) 1; Los Gatos (USNM) 1; Strawberry Canyon (Campus Univ. of Calif.)? Berkeley, Alameda Co., October (FMNH) 1; Evey Can., San Gabriel Mts., N of Claremont, June (INHS) 1. *Florida*: Jacksonville (AMNH) 1; Ocala, Marion Co., April (JHFC) 4. *Illinois*: Chicago (USNM) 3. *Iowa*: Iowa City (USNM) 1; state label only (FMNH) 1. *Kansas*: Lawrence (AMNH) 1. *Louisiana*: Natalbany, June (USNM) 4. *Maryland*: Edgewood, November (CUIC) 1; state label only (DEFW) 1. *Massachusetts*: W. Roxbury, January (MCZC) 1. *New York*: Olcott, October (CUIC) 1; Ithaca (USNM) 1; New York, March (USNM) 1. *North Carolina*: Raleigh, August (NCSC) 1. *Ohio*: Vinton Co., Lake Hope, November (FMNH) 1. *Texas*: Bastrop St. Park, nr. Bastrop, June (ERHC) 10. *Virginia*: Munden, May (MCZC) 1; Newport, Giles Co., August (JHFC) 1. *Washington*: Seattle (intercept Japan, lily bulbs) (UCRC) 1.



*Habitat.* Adults of this species have been collected from along a stream bed, from under logs, from oak and pine duff, and from a blacklight trap.

*Myrmecocephalus gracilis* (Casey), **Revised Status**

Figs. 5, 85, 106; Map 5

*Lorinota gracilis* Casey, 1906, p. 244 [type locality, North Carolina, Tryon].

*Myrmecocephalus gracilis*; Moore and Legner, 1975, p. 415 (as synonym of *cingulatus*).

*Lorinota parva* Casey, 1906, p. 244 [type locality, Florida, Enterprise]. **New Synonym.**

*Diagnosis.* Adults of this species are extremely similar to those of *M. concinnus* in color and size, but may be distinguished by the basal impression of abdominal tergite III often with distinct punctures, and the broadly rounded basal angles of the pronotum.

*Description.* Length 2.0–3.0 mm (N = 22;  $\bar{x}$  = 2.39 mm). Color light to dark rufo-testaceous; three basal and apical antennal segments, mouthparts, humeri, apices of elytra, basal 2 abdominal segments, tibiae and tarsi paler. Habitus as in Figure 5.

Head (Fig. 5) moderate in size, convex, nearly as broad as prothorax at broadest part, broadly arcuate-truncate at base, hind angles broadly rounded. Surface sparsely and minutely punctured and pubescent; surface between punctures smooth and shining. Eyes as long as temples. Antenna moderately short, stout, reaching middle of elytra. Prothorax (Fig. 5) elongate, slightly longer than head, broadest at anterior third, gradually converging posteriorly; basal margin evenly convex, very narrowly reflexed; basal angles not produced, broadly rounded. Disc deeply sulcate along median line, except at extreme apex, sulcus ending in a deep, round subbasal fovea. Surface sparsely and finely punctured and pubescent; punctures more coarse and asperate near sulcus; surface between punctures smooth and shining. Scutellum finely carinate at base; surface densely and coarsely punctured and pubescent. Elytra with surface sparsely, minutely and uniformly punctured and pubescent; surface between punctures smooth and polished. Abdomen broad at base, much narrower than elytra. Tergum III strongly and broadly impressed at base; terga IV and V moderately impressed at base. Impression of tergum III with coarse, well-separated punctures at the middle in most specimens; impressions of terga IV and V usually impunctate or with few subobsolete punctures. Tergal surfaces densely and coarsely punctured and pubescent; surface between punctures with minute microsculpture consisting of fine, transverse microlines.

*Male.* Eighth tergite with apical margin broadly truncate, simple. Apical margin of eighth sternite broadly, evenly rounded. Median lobe of aedeagus as in Figure 85A. Paramere as in Figure 85B.

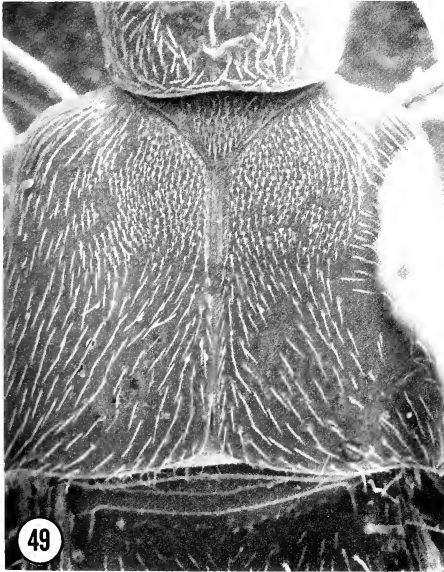
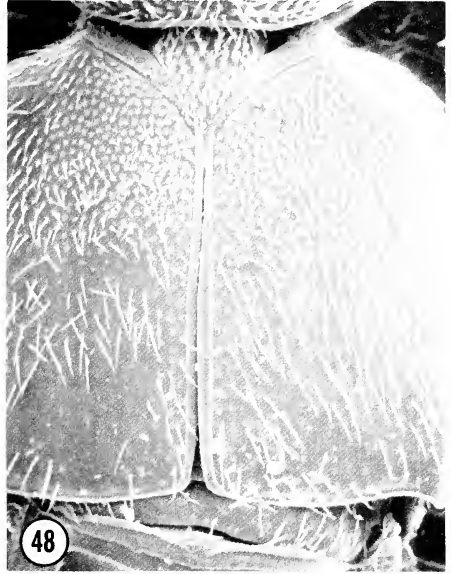
*Female.* Eighth tergite and sternite with apical margin as in male. Spermatheca as in Figure 106.

*Type material.* *Lorinota gracilis* Casey. Holotype, with labels as follows: "Tryon NC"/Pinus/CASEY bequest 1925/Type USNM 38917/"gracilis Csy."

*Lorinota parva* Casey. Holotype with the following labels: "erprise, Fla." (=Enterprise)/CASEY bequest 1925/Type USNM 38918/"parva Csy."

Type specimens of the above two species are in the Casey collection of the U.S. National Museum (Natural History), Washington.





Figs. 47–50. Elytra of North American Falagriini, dorsal aspect. 47. *Falagria dissecta*. 48. *Falagrioma thoracica*. 49. *Lissagria laeviuscula*. 50. *Borboropora quadriceps*.

cypress logs in Florida, a rotting saguaro cactus in Arizona, and incandescent light and blacklight traps in Florida.

***Myrmecocephalus sculpturatus*, new species**

Figs. 6, 64, 65, 71, 86, 107; Map 6

*Diagnosis.* This species is one of the most distinctive of the genus in America north of Mexico; it can be readily recognized by the presence of reticulate microsculpture on the dorsal body surfaces (Fig. 64).

*Description.* Length 3.4–3.9 mm (N = 6;  $\bar{x}$  = 3.71 mm). Color light to dark rufo-testaceous; mouthparts, antennal segments, legs and tarsi paler. Habitus as in Figure 6.

Head moderate in size, slightly longer than broad, lateral margins broadly and evenly rounded, broadly rounded at base. Surface behind antennal fossae slightly but broadly depressed and with conspicuous reticulate microsculpture, shining. Eyes much shorter than length of temples. Antenna moderately long, reaching apex of elytra. Prothorax (Fig. 6) elongate, longer than head; anterior angles broadly and evenly rounded; lateral margins narrowed and converging to base; posterior margin broadly convex, finely margined and reflexed. Disc deeply sulcate along median line, except at extreme apex, sulcus ending in a round, deep, subbasal fovea. Surface finely and sparsely punctured and pubescent; surface between punctures with fine reticulate microsculpture (Fig. 64). Scutellum with broad carina at base, surface coarsely and moderately densely punctured and pubescent, also with reticulate microsculpture. Elytra with surface between punctures with fine but distinct reticulate microsculpture (as in Fig. 64). Abdomen broad at base, nearly as broad as elytra. Terga III–V transversely impressed at base; impression of tergum III coarsely punctured. Tergal surfaces rather densely punctured and pubescent; surface between punctures coarsely shagreened (Fig. 65).

*Male.* Eighth tergite with apical margin arcuate-truncate. Eighth sternite with apical margin broadly and evenly rounded. Median lobe of aedeagus as in Figure 86A. Paramere as in Figure 86B.

*Female.* Eighth tergite and sternite with apical margin as in male. Spermatheca as in Figure 107.

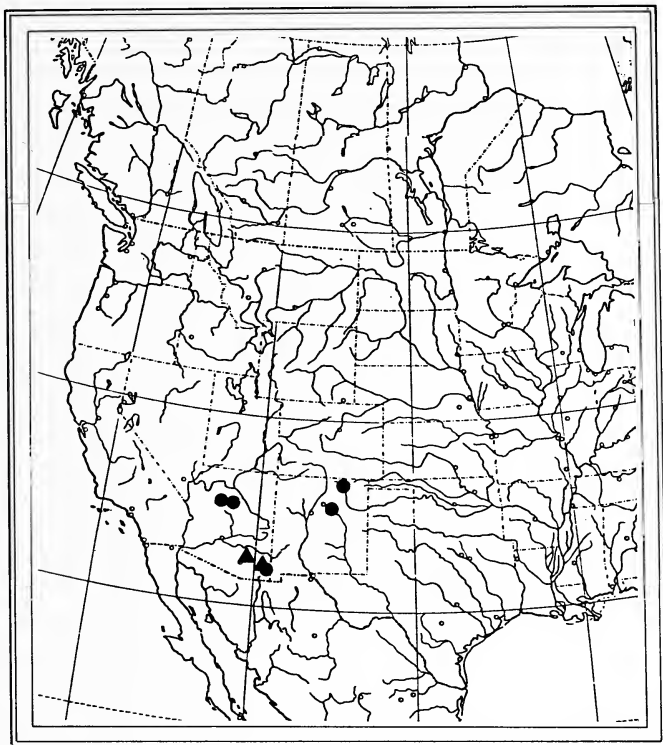
*Type material.* Holotype, male, with labels: USA: Ariz., Cochise Co., W. Slope Chiricahua Mts., Barfoot Peak, 8,250 ft, V-4-1968/Under bark of log, L. Herman/HOLOTYPE *Myrmecocephalus sculpturatus* n. sp., E. R. Hoebeke 1981. The type is deposited in the collection of the American Museum of Natural History (AMNH), New York, NY.

Paratypes, 5, in the collections of the American Museum of Natural History, and the Field Museum of Natural History, Chicago.

*Distribution.* *Myrmecocephalus sculpturatus* at present is known only from the mountains of southeastern Arizona (Map 6) at elevations of 8,250–8,500 feet. Specimens have been collected in May.

*Material examined.* 6 specimens. UNITED STATES. *Arizona:* Cochise Co., W. Slope Chiricahua Mts., Barfoot Peak, 8,250 ft, May (AMNH) 3; St. Catalina Mts., 8,500 ft, May (FMNH) 3.





Map 6. Distribution of *M. sculpturatus* (triangles) and *M. caviceps* (circles).

**Habitat.** Little is known about the habitat of this species. Specimens at hand have been collected from under bark.

**Etymology.** The specific epithet is derived from the Latin *sculpto*, *sculptus*, meaning to carve, engrave, or cut, and referring to the reticulate microsculpture on the dorsal body surfaces.

*Myrmecocephalus arizonicus* (Casey)

Figs. 7, 66, 87, 108; Map 7

*Lorinota arizonica* Casey, 1906, p. 241 [type locality, Arizona, Williams].

*Myrmecocephalus arizonica*; Moore and Legner, 1975, p. 415.

*Lorinota acomana* Casey, 1906, p. 242 [type locality, New Mexico, Cloudcroft].

*Lorinota fontinalis* Casey, 1906, p. 242 [type locality, Colorado, Colorado Springs].

**Diagnosis.** Adults of *M. arizonicus* can be distinguished from those of other species of the genus by the complete absence of microsculpture on the dorsal body surfaces (Fig. 66); the integument is smooth and shining between punctures.

**Description.** Length 3.1–3.9 mm (N = 98;  $\bar{x}$  = 3.42 mm). Color uniformly pale



rufo-piceous; mouthparts, basal antennal segments and legs usually paler. Habitus as in Figure 7.

Head (Fig. 6) moderate in size, broadly arcuate-truncate at base; hind angles broadly rounded. Surface flattened behind antennae to occiput, sparsely and very minutely punctured and pubescent; surface between punctures smooth and shining. Eyes slightly prominent, much shorter than length of temples. Antenna moderately long, slightly incrassate distally, nearly reaching to first abdominal segment. Prothorax (Fig. 6) elongate, distinctly narrower than head, evenly convex dorsally, strongly converging to base; posterior margin finely reflexed. Disc deeply sulcate along median line except at extreme apex, sulcus ending in a round, deep, subbasal fovea. Surface moderately sparsely and minutely punctured and pubescent; punctures slightly more asperate and coarse towards sulcus; surface between punctures smooth and polished. Scutellum broadly carinate at base along median line, not extending to apex; surface densely and coarsely punctured and pubescent. Elytra with surface moderately sparsely, minutely and uniformly punctured and pubescent; surface between punctures smooth and shining. Abdomen relatively broad at base, narrower than elytra. Terga III–V broadly and transversely impressed at base; impressions coarsely and densely punctured. Tergal surfaces moderately densely and finely punctured and pubescent; punctures more asperate on basal segments; surface (Fig. 66) between punctures smooth and shining.

*Male.* Eighth tergite with apical margin truncate, simple. Eighth sternite with apical margin broadly rounded. Median lobe of aedeagus as in Figure 87A. Paramere as in Figure 87B.

*Female.* Eighth tergite and sternite with apical margin as in male. Spermatheca as in Figure 108.

*Type material.* *Lorinota arizonica* Casey. Lectotype, here designated, with labels as follows: "Ari." [=Williams, Arizona, Mr. H. F. Wickham]/CASEY bequest 1925/Type USNM 38912/"arizonica Csy."; my lectotype designation label is attached to it. Two other paralectotypes have labels identical to the lectotype.

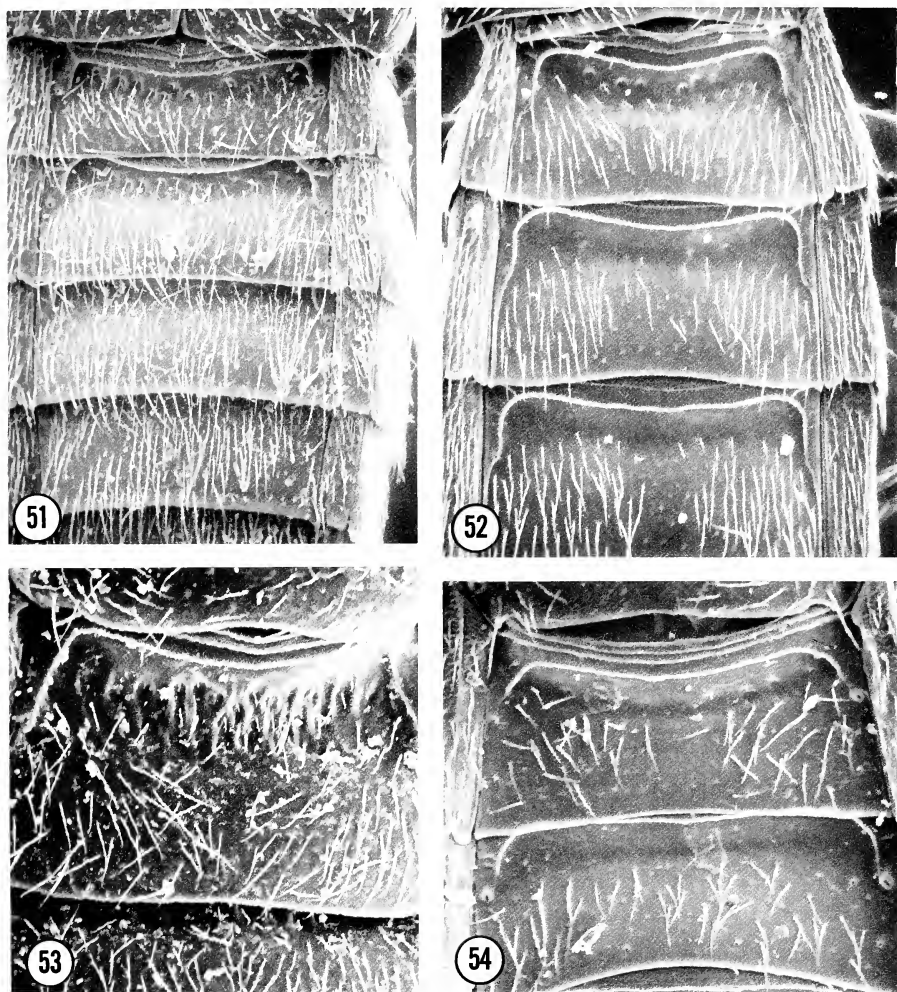
*Lorinota acomana* Casey. Lectotype, here designated, with the following labels: "Cloudcroft, New Mex.)/CASEY bequest 1925/Type USNM 38913/"acomae Csy."; my lectotype designation label is attached to it. Three other paralectotypes also have labels identical to the lectotype.

*Lorinota fontinalis* Casey. Lectotype, here designated, with labels as follows: "Colo. Spr., Col., H. F. Wickham, June 15–30 '96, 6,000–7,000 ft.)/CASEY bequest 1925/Type USNM 38914/"fontinalis Csy."; my lectotype designation label is attached to it. One paralectotype has labels identical to the lectotype.

Type specimens of the above 3 species are in the Casey collection of the U.S. National Museum (Natural History), Washington.

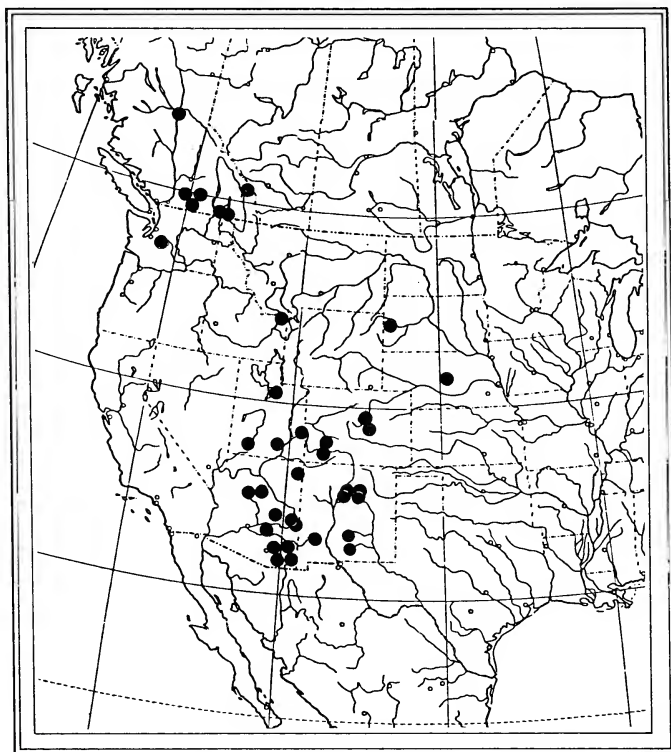
*Distribution.* *Myrmecocephalus arizonicus* is widely distributed in western North America (especially at higher elevations), from southern British Columbia south through the mountains of Idaho, Utah, Colorado, Arizona and New Mexico (Map 7). Specimens have been collected from March through October.

*Material examined.* 661 specimens. CANADA: *British Columbia*: 7 mi N of Oliver, June (CNCI) 1; McLeod Meadows, Kootenay Nat'l. Pk., July (CNCI) 9; Kimpton Cr., Kootenay Nat'l. Pk., 4,000 ft, July (CNCI) 1; Prince George, May (CNCI) 1; 4



Figs. 51–54. Basal abdominal segments of North American Falagriini, dorsal aspect. 51. *Cordalia obscura*. 52. *Falagriota occidua*. 53. *Myrmecocephalus cingulatus*. 54. *M. concinnus*.

mi W of Midway, June (CNCI) 1; Vernon, May (CNCI) 1; Pillar Lake, June (CNCI) 2; 2 mi S of Salmo, June (CNCI) 1; Creston, March, April, May (CNCI, MCZC, CUIC) 38; Midday Val., Merritt, June (INHS) 3. UNITED STATES: *Arizona*: Graham Co., Pinaleno Mts., Wet Canyon, 6,000–6,100 ft, July (CNCI) 9; Cochise Co., Chiric. Mts., Rustler Park, 8,400 ft, July (CNCI) 11; Graham Co., Pinaleno Mts., Post Crk., 9,000 ft, July (CNCI) 1; Graham Co., Pinaleno Mts., Turkey Flat, 7,200 ft, July (CNCI) 6; Apache Co., Chuska Mts., 2,250 m, Wagonwheel Campgrnd., July (CNCI) 2; Apache Co., Chuska Mts., 8,500 ft, August (MCZC) 2; Apache Nat'l. For., 2,700 m, Big Lake, 22 mi SW of Eagar, July (CNCI) 4; Coconino Co., San Francisco



Map 7. Distribution of *M. arizonicus*.

Mts., Snow Bowl, 2,800 m, July (CNCI) 1; Navajo Co., 2 mi W of Black Lake, Sitgreaves Nat'l. For., 2,240 m, July (CNCI) 26; Gila Co., Pinal Mts., Pioneer Pass, 1,660 m, July (CNCI) 1; Apache Nat'l. For., Escudilla Mt., 2,840 m, 9 mi NE of Alpine, July (CNCI) 1; Apache Nat'l. For., Escudilla Mt., 2,730 m, 8 mi NE of Alpine, July (CNCI) 1; Navajo Co., Sitgreaves Nat'l. For., Willow Springs Canyon, 2,160 m, July (CNCI) 1; Graham Co., Pinaleno Mts., 4 mi NW of Columbine, 8,800 ft, July (CNCI) 3; Cochise Co., Parker Canyon Lake, 5,500 ft, July (CNCI) 1; Graham Co., Pinaleno Mts., Grank Crk., 8,500 ft, July (CNCI) 5; Cochise Co., Carr Canyon, Huachuca Mts., 2,150 m, July (CNCI) 1; Cochise Co., Huachuca Mts., Miller Canyon, 5,500 ft, August (CNCI) 13; Cochise Co., 2 mi SW Portal, August (MCZC) 1; Cochise Co., nr. Portal, Chiricahua Mts., Rustler Park, 8,400 ft, July (FMNH) 1; Williams (FMNH, MCZC, USNM) 5; Graham Co., Wet Canyon, June (FMNH) 2; White Mts., Hannegans Meadow, May (FMNH) 2; Flagstaff (FMNH) 1; Graham Mts., May (FMNH) 1; St. Catalina Mts., 8,000 ft, May (FMNH) 1; Cochise Co., W Slope Chiric. Mts., Barfoot Peak, 8,250 ft, May (AMNH) 11; Cochise Co., Chiricahua Mts., Rustlers Park, 8,400 ft, May (AMNH) 1; Graham Co., Pinaleno Mts., Mile Post 127, 6,500 ft, May (AMNH) 22; Cochise Co., Ash Spring, Chiricahua Mts., May (AMNH) 4; St. Catalina Mts., 7,000 ft, 8,000 ft, April, May (AMNH) 3; Cochise Co., Chiricahua



Mts., Rustler Park, August (AMNH) 1; Cochise Co., Ramsey and Carr Canyons, Huachuca Mts., 6,500–7,000 ft, May (AMNH) 12; Cochise Co., Chiric. Mts., nr. Flys Peak, May (AMNH) 1; Cochise Co., 3 mi S of SWRS, Greenhouse Cny., Chiric. Mts., 5,500 ft, May (AMNH) 5; Flagstaff, San Francisco Mts., about 8,000 ft, August (AMNH) 1; Bear Wallow, Mt. Lemmon, May (CUIC) 6; Pima Co., Bear Wallow, Santa Catalina Mts., 8,200 ft, July (MSUC) 1; Cochise Co., Chiricahua Mts., Rustler Park, August (UCRC) 1; Marshall Gulch, St. Catalina Mts., August (URCI) 1; Chiric. Mts., May, June (USNM) 11; Flagstaff (CASC) 1; Santa Catalina Mts., 7,700 ft, August (CASC) 1; San Francisco Mts. (CASC) 2; state label only (USNM) 1. *Colorado*: Lime Creek, 9,500 ft, 6 mi S of Molas Pass, July (CNCI) 8; Durango, Missionary Ridge Road, 10,300 ft, July (CNCI) 1; Durango, March (USNM) 2; Ouray (AMNH, MCZC, USNM, CASC, FMNH) 45; Ouray, 7,500–8,000 ft, July (USNM) 1; above Ouray, Toll Road, 8,000–9,000 ft (USNM) 1; Denver, October (USNM) 2; Colorado Springs (USNM) 6; Waldo Canon, July (USNM) 1; state label only (MCZC) 10. *"Dakota"*: state label only, Dac. (DEFW) 1. *Idaho*: Fremont Co., Warm River, August (JHFC) 2. *Nebraska*: state label only, Neb. (DEFW) 1. *New Mexico*: Lincoln Nat'l. For., 2 mi SE of Cloudcroft, 8,500 ft, July (CNCI) 98; Sandia Mts., 6,500 ft, Cibola Nat'l. For., Las Huertas Crk., July (CNCI) 1; Sandia Mts., 8,500 ft, Cibola Nat'l. For., Tree Spring Trail, July (CNCI) 14; Sandia Mts., Cibola Nat'l. For., Sandia Crest, 10,000–10,500 ft, July (CNCI) 49; Lincoln Nat'l. For., 1 mi SE of Cloudcroft, 8,750 ft, July (CNCI) 5; Cloudcroft, 8,500 ft, July (CNCI) 73; Coolidge (USNM, FMNH) 4; Iron Creek For. Camp, Black Range, August, September (FMNH) 2; Cloudcroft (USNM, MCZC) 8; Cloudcroft, June, August (USNM, MCZC) 4; Porvenir (CASC, MCZC) 42; Las Vegas HS, August (USNM, MCZC) 8; Beulah (MCZC) 1; Lincoln Co., Bonita Creek, 8 mi W of Angus, 7,700 ft, July (AFNC) 1; Jemez Mts., May, August, October (CASC) 4; state label only (FMNH) 1. *South Dakota*: Lawrence Co., Black Hills N.F., Roubaix Lk. Cpgd., 5,500 ft, July (MCZC) 1. *Utah*: Lonesome Beaver, 7,500 ft, Henry Mts., July (CNCI) 4; La Sal Mts., August, Grand Co., Poplar zone–8,500 ft (FMNH) 1; Iron Co., 5 mi SE of Cedar City, August (AMNH) 1; Park City, June (USNM) 1; Alta, June (USNM) 1; "Am. Fk. Can.," June (USNM) 1. *Washington*: Pierce Co., Mt. Rainier, N.P., 2 mi W Jct. Wash. 706 & Wash. 123, 2,600 ft, July (MCZC) 1.

*Habitat*. Specimens at hand have been taken from under the bark of logs, from leaf litter, from flood debris and wet moss, from soil along a stream, from fungus (*Fomitopsis pinicola*, *Fomes robineae*), and from a squirrel midden.

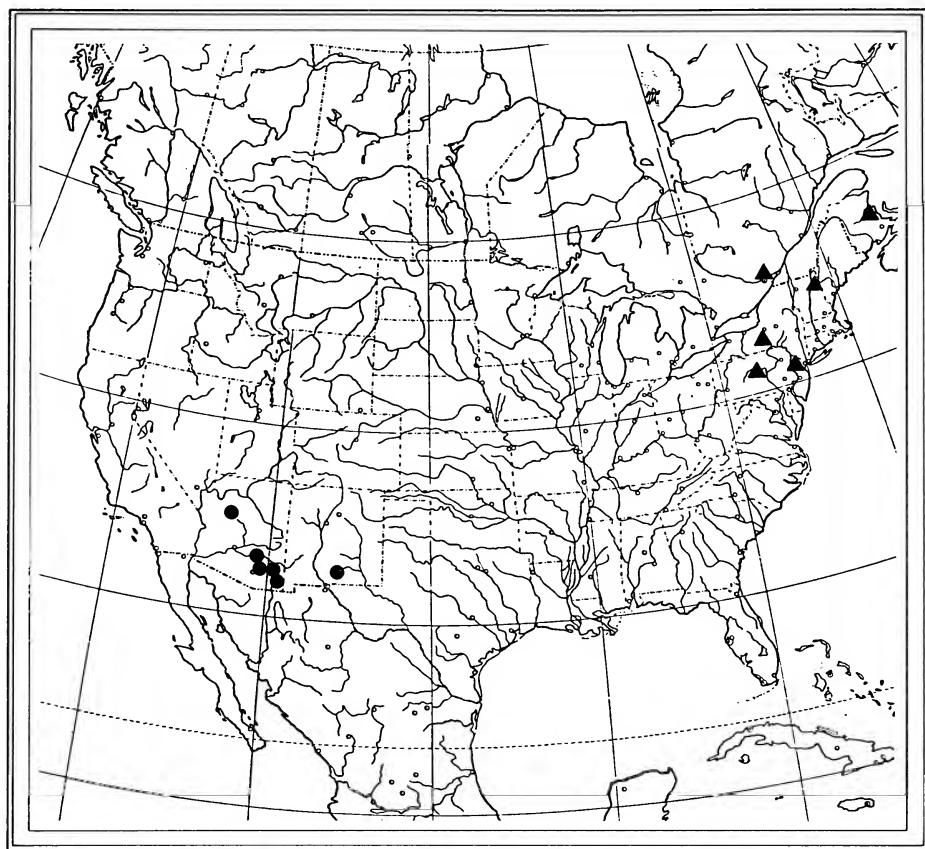
***Myrmecocephalus gatineauensis*, new species**

Figs. 8, 55, 67, 88, 109; Map 8

*Diagnosis*. Adults of *M. gatineauensis* closely resemble those of *arizonicus* but are distinguishable by the presence of transverse microsculpture (Fig. 67) on the abdominal terga, and an allopatric northeastern distribution.

*Description*. Length 2.9–3.9 mm (N = 56;  $\bar{x}$  = 3.28 mm). Color light to dark brownish-piceous; mouthparts, basal antennal segments and legs generally paler; apical abdominal segments sometimes darker, piceous. Habitus as in Figure 8.

Head (Fig. 8) moderate in size, flattened dorsally behind antennae, slightly longer than broad, broadly and evenly rounded at base. Surface densely and very finely



Map 8. Distribution of *M. gatineauensis* (triangles) and *M. pinalicus* (circles).

punctured and pubescent; surface between punctures smooth and shining. Eyes prominent, shorter than length of temples. Antenna relatively long, extending to apex of elytra. Prothorax (Fig. 8) elongate, cylindrical, strongly and evenly convex dorsally, broadest across anterior third; anterior angles broadly rounded; lateral margins strongly converging to base, slightly sinuate beyond middle; posterior margin narrowly reflexed. Disc deeply sulcate along median line, except extreme apex, sulcus ending in a deep, round, subbasal fovea. Surface densely and very finely punctured and pubescent; punctures coarser and slightly asperate towards sulcus; surface between punctures smooth and shining. Scutellum broadly carinate along median line at base only, carina not extending to apex; surface densely, coarsely punctured and pubescent. Elytra with surface moderately densely, coarsely, and uniformly punctured and pubescent; surface between punctures smooth and shining. Abdomen (Fig. 55) broad at base, narrower than elytra at base. Terga III and IV broadly and deeply impressed at base; tergum V shallowly impressed at base. Impression of tergum III coarsely punctured (Fig. 55); impressions of terga IV and V obsolete punctured. Tergal



surfaces rather densely and coarsely punctured and pubescent; surface between punctures with very fine microsculpture of minute, wavy, transverse microlines (Fig. 67).

*Male.* Eighth tergite with apical margin broadly truncate. Apical margin of eighth sternite broadly rounded. Median lobe of aedeagus as in Figure 88A. Paramere as in Figure 88B.

*Female.* Eighth tergite and sternite with apical margin as in male. Spermatheca as in Figure 109.

*Type material.* Holotype, male, labeled: QUE: Gatineau Pk. near Mud Lake, 24.X.1967, A. Smetana/HOLOTYPE *Myrmecocephalus gatineauensis* n. sp., E. R. Hoebeke 1981. The type is in the Canadian National Collection, Ottawa.

Paratypes, 63, in the collections of the Canadian National Collection; American Museum of Natural History, New York, NY; Museum of Comparative Zoology, Harvard University, Cambridge, MA; Cornell University, Ithaca, NY; and California Academy of Sciences, San Francisco, CA.

*Distribution.* *Myrmecocephalus gatineauensis* occurs in northeastern North America, from New Brunswick and Quebec south to central Pennsylvania and northern New Jersey (Map 8). Specimens have been collected in May and from August through November.

*Material examined.* 64 specimens. CANADA: *New Brunswick:* Kouchibouguac Nat'l. Pk., September (CNCI) 4. *Quebec:* 4 mi W of Masham, nr. Mud Lake, August, October (CNCI) 21; Blind Lake, Gatineau Park, November (CNCI) 6; Fortune Lake, Gatineau Park, November (CNCI) 16; Gatineau Park, nr. Mud Lake, October (CNCI) 9; Gatineau Park, Hay Lake, October (CNCI) 4; 1 mi SW of Meach Lake, Gatineau Park, November (CNCI) 1. UNITED STATES: *New Hampshire:* Franconia (AMNH) 1. *New Jersey:* Phillipsburg, May (CASC) 1. *New York:* Tompkins Co., Snyder Heights, Ithaca, May (ERHC) 1. *Pennsylvania:* state label only (MCZC) 1.

*Habitat.* Adults of this species have been taken from a berlese sample of the nest lining of a deserted beaver lodge in Quebec, and from a blacklight trap in New York.

*Etymology.* *Gatineauensis* is an adjective derived from Gatineau N.C.C. Park, the place of origin for the majority of the specimens comprising the type series.

*Myrmecocephalus caviceps* (Casey)

Figs. 9, 68, 89, 110; Map 6

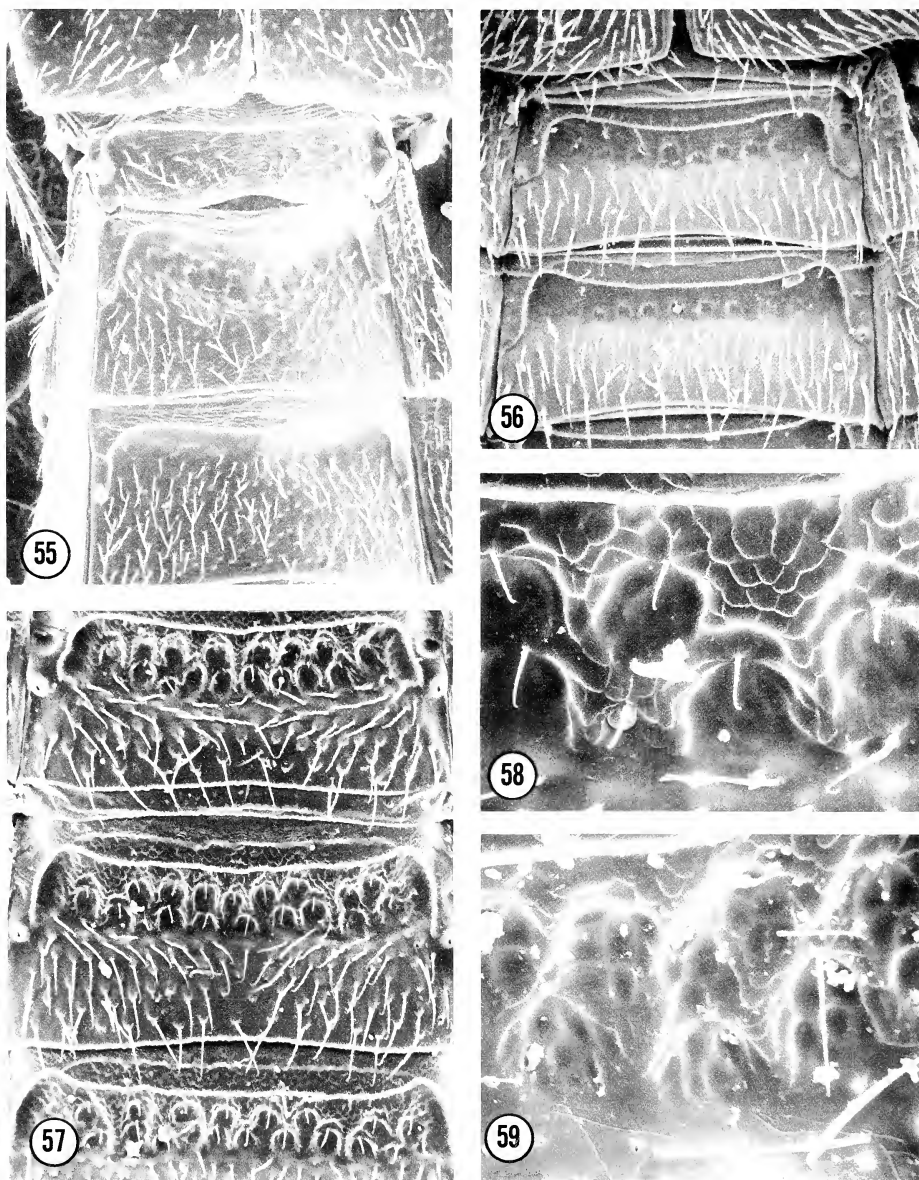
*Lorinota caviceps* Casey, 1906, p. 240 [type locality, New Mexico, Las Vegas].

*Myrmecocephalus caviceps*; Moore and Legner, 1975, p. 415.

*Diagnosis.* Adults of this species are very similar in appearance to those of *M. pinalicus* from which they are readily distinguished by the presence of fine transverse microsculpture on the elytral disc, similar to that found on the abdominal terga (Fig. 68).

*Description.* Length 2.9–3.4 mm ( $N = 11$ ;  $\bar{x} = 3.2$  mm). Color light to dark piceous-brown; mouthparts, basal antennal segments and legs paler. Habitus as in Figure 9.

Head (Fig. 9) moderate in size, slightly longer than broad, broadly arcuate-truncate at base. Surface moderately sparsely and minutely punctured and pubescent; surface between punctures smooth and shining. Eyes prominent, shorter than length of temples. Antenna moderate in length, rather stout, reaching to about middle of elytra. Prothorax (Fig. 9) elongate, evenly and strongly convex dorsally, broadest across



Figs. 55–59. Basal abdominal segments of North American Falagriini, dorsal aspect. 55. *Myrmecocephalus gatineauensis*. 56. *Falagria dissecta*. 57. *Aleodorus scutellaris*. 58–59. Close-up magnification of large foveae of basal abdominal impression of tergum III. 58. *Aleodorus scutellaris*. 59. *Aleodorus intricatus*.

anterior third; anterior angles broadly rounded; lateral margins strongly converging to base; posterior margin broadly arcuate, finely reflexed. Disc deeply sulcate along median line except at extreme apex, sulcus ending in a deep, rounded subbasal fovea. Surface sparsely and relatively minutely punctured and pubescent; surface between punctures smooth and shining. Scutellum finely carinate at base along median line; surface otherwise densely and coarsely punctured and pubescent. Elytra with surface moderately sparsely, finely and uniformly punctured and pubescent; surface between punctures with fine microsculpture consisting of minute transverse interconnecting microlines (similar to that in Fig. 68). Abdomen broad at base, narrower than elytra. Terga III–V transversely impressed at base; impression of tergum III with coarse and somewhat obsolete punctures; impressions of terga IV and V impunctate. Tergal surfaces relatively sparsely and finely punctured and pubescent; surface between punctures with fine microsculpture (Fig. 68), similar to that of elytra.

*Male.* Eighth tergite with apical margin broadly truncate, simple. Eighth sternite with apical margin broadly rounded. Median lobe of aedeagus as in Figure 89A. Paramere as in Figure 89B.

*Female.* Eighth tergite and sternite with apical margin as in male. Spermatheca as in Figure 110.

*Type material.* Lectotype, here designated, with labels as follows: "N.M." [=Las Vegas, Mr. Herman Meeske]/CASEY bequest 1925/Type USNM 38911/"*caviceps* Csy."; my lectotype designation label is attached to it. In addition, two paralectotypes have labels identical to the lectotype, while one other is with labels: "Webb voir, Flagstaff, Ar.," All specimens are in the Casey collection of the U.S. National Museum (Natural History), Washington.

*Distribution.* *Myrmecocephalus caviceps* occurs at the high elevations of Arizona and New Mexico (7,600–8,500 ft) (Map 6). Adults have been collected from April to September, with most specimens taken in July and August.

*Material examined.* 12 specimens. UNITED STATES: *Arizona*: Cochise Co., Chiricahua Mts., Rustlers Park, April (AMNH) 2; Rustlers Park, 8,400 ft, July (CNCI) 1; Rustlers Park, 8,400 ft, July (FMNH) 1; Rustlers Park, August, 8,000 ft (FMNH) 1; Rustlers Park, 8,300 ft, September (FMNH) 1; nr. Portal, Onion Saddle, August (FMNH) 1; Chiricahua Mts., 8,500 ft, May (FMNH) 1; Williams, June (USNM) 1. *New Mexico*: Koehler (USNM) 1.

*Habitat.* Little is known about the habitat of this species. Specimens at hand have been collected from under bark of a dead ponderosa pine.

### *Myrmecocephalus pinalicus* (Casey), **Revised Status**

Figs. 10, 40, 69, 90, 111; Map 8

*Lorinota pinalica* Casey, 1906, p. 241 [type locality, Arizona, Pinal Mts.].

As synonym of *caviceps*: Fenyès, 1912, p. 27; 1920, p. 158.

*Myrmecocephalus pinalica*; Moore and Legner, 1975, p. 415 (as synonym of *caviceps*).

*Diagnosis.* This species is extremely similar to *M. caviceps* from which it is distinguished by the complete absence of microsculpture on the elytral disc.

*Description.* Length 2.7–3.2 mm (N = 18;  $\bar{x}$  = 2.95 mm). Color light to very dark rufo-piceous; mouthparts, antennae and legs paler. Habitus as in Figure 10.



Head (Fig. 10) moderate in size, slightly longer than broad, broadly rounded at base. Surface very sparsely and finely punctured and pubescent (appearing nearly impunctate); surface between punctures smooth and shining. Eyes prominent, shorter than length of temples. Antenna moderately stout, reaching nearly to apex of elytra. Prothorax (Fig. 10) distinctly elongate, cylindrical, nearly as long as head, broadest across anterior third; anterior angles broadly and evenly rounded; lateral margins strongly converging to base; posterior margin finely but distinctly reflexed. Disc deeply sulcate along median line except at extreme apex, sulcus ending in a deep, round subbasal fovea. Surface sparsely and very finely punctured and pubescent; surface between punctures smooth and polished. Scutellum finely carinate basally; surface moderately densely and coarsely punctured and pubescent; extreme apex smooth and impunctate. Elytra with surface evenly, relatively sparsely and finely punctured and pubescent; surface between punctures smooth and polished. Abdomen broad at base, narrower than elytra. Tergum III broadly impressed at base; terga IV and V shallowly impressed basally. Impression of tergum III with coarse and somewhat dense punctures; impressions of terga IV and V impunctate or with few obsolete punctures. Tergal surfaces very sparsely and finely punctured and pubescent; surface between punctures with sparse and fine transverse microsculpture (Fig. 69).

*Male.* Eighth tergite with apical margin truncate, simple. Apical margin of eighth sternite broadly, evenly rounded. Median lobe of aedeagus as in Figure 90A. Paramere as in Figure 90B.

*Female.* Eighth tergite and sternite with apical margin as in male. Spermatheca as in Figure 111.

*Type material.* Holotype, with labels as follows: "Pinal Mts., Arizona, Wickham"/CASEY bequest 1925/Type USNM 38910/"Lorinota pinalica Csy." The specimen is in the Casey collection of the U.S. National Museum (Natural History), Washington.

*Distribution.* *Myrmecocephalus pinalicus* is known from the high elevations of Arizona and New Mexico (Map 8). Adults have been collected from May through August.

*Material examined.* 22 specimens. UNITED STATES. *Arizona:* Graham Co., Pinaleno Mts., Turkey Flat, 7,200 ft, July (CNCI) 1; Cochise Co., Rucker Dam, Chiricahua Mts., August (UCRC) 1; Pima Co., Santa Catalina Mts., Catalina Hwy., 7,000 ft, May (AMNH) 8; St. Catalina Mts., 8,000 ft, May (AMNH) 1; Chiricahua Mts., June (USNM) 1; Williams (FMNH) 1; Cochise Co., 3 mi S of SWRS, Greenhouse Cyn., Chiricahua Mts., 5,500 ft, May (AMNH) 1; state label only (MCZC, FMNH, USNM) 7. *New Mexico:* Cloudcroft, May (FMNH) 1.

*Habitat.* Some specimens at hand have been taken from under bark of a ponderosa pine log.

#### 4. *Falagria* Leach

*Falagria* Leach, 1819, p. 177; Curtis, 1829, p. 33; 1833, pl. 462; Mannerheim, 1831, p. 500; Stephens, 1832, p. 103; Dejean, 1833, p. 74; 1837, p. 83; Erichson, 1839, p. 293; 1840, p. 48; Redtenbacher, 1849, p. 650; Melsheimer, 1853, p. 153; Lacordaire, 1854, p. 28; Jacquelin du Val, 1857, p. 4; Kraatz, 1856, p. 32; Redtenbacher, 1858, p. 118; Thomson, 1859, p. 34; 1860, p. 297; LeConte, 1863, p. 22;

Gemminger and Harold, 1868, p. 502; Crotch, 1873, p. 28; Redtenbacher, 1874, p. 129; Mulsant and Rey, 1875, p. 433; LeConte and Horn, 1883, p. 91; Henshaw, 1885, p. 31; Fowler, 1888, p. 147; Ganglbauer, 1895, p. 253; Everts, 1898, p. 231; 1903, p. 231; Casey, 1906, pp. 227, 245; Reitter, 1909, pp. 41, 74; Blatchley, 1910, pp. 345, 346; Fenyès, 1912, p. 20; Johansen, 1914, pp. 237, 238; Fenyès, 1918, p. 18; 1920, p. 152; Cameron, 1920, pp. 361, 392; Leng, 1920, p. 124; Notman, 1920, p. 731; Everts, 1922, p. 103; Bernhauer and Scheerpeltz, 1926, p. 574; Porta, 1926, p. 150; Portevin, 1929, pp. 253, 293; Scheerpeltz, 1929, p. 9; 1930, p. 73; Bradley, 1930, p. 85; Joy, 1932, pp. 16, 39, 41; Rapp, 1933, p. 402; Scheerpeltz, 1934, p. 1572; Cameron, 1939, pp. 233, 242; Blackwelder, 1943, p. 547; 1944, p. 158; Tottenham, 1949, p. 387; Horion, 1951, p. 169; Blackwelder, 1952, p. 164; Hansen, 1954, p. 96; Tottenham, 1957, pp. 89, 90; Scheerpeltz, 1958, p. 35; Horion, 1967, p. 202; Arnett, 1968, p. 289; Palm, 1968, pp. 71, 77; Scheerpeltz, 1974, pp. 51, 222; Lohse, 1974, pp. 65, 66; Moore and Legner, 1975, p. 414; SeEVERS, 1978, p. 144; Last, 1979, p. 233.

Variant spellings: *Falagrea* Eichelbaum, 1915, p. 116; *Flagria* Pearse, 1946, p. 139.

*Type-species: Staphylinus sulcatus* Paykull, fixed by original designation.

*Coenobites* Gistel, 1856, p. 387; Blackwelder, 1952, p. 102.

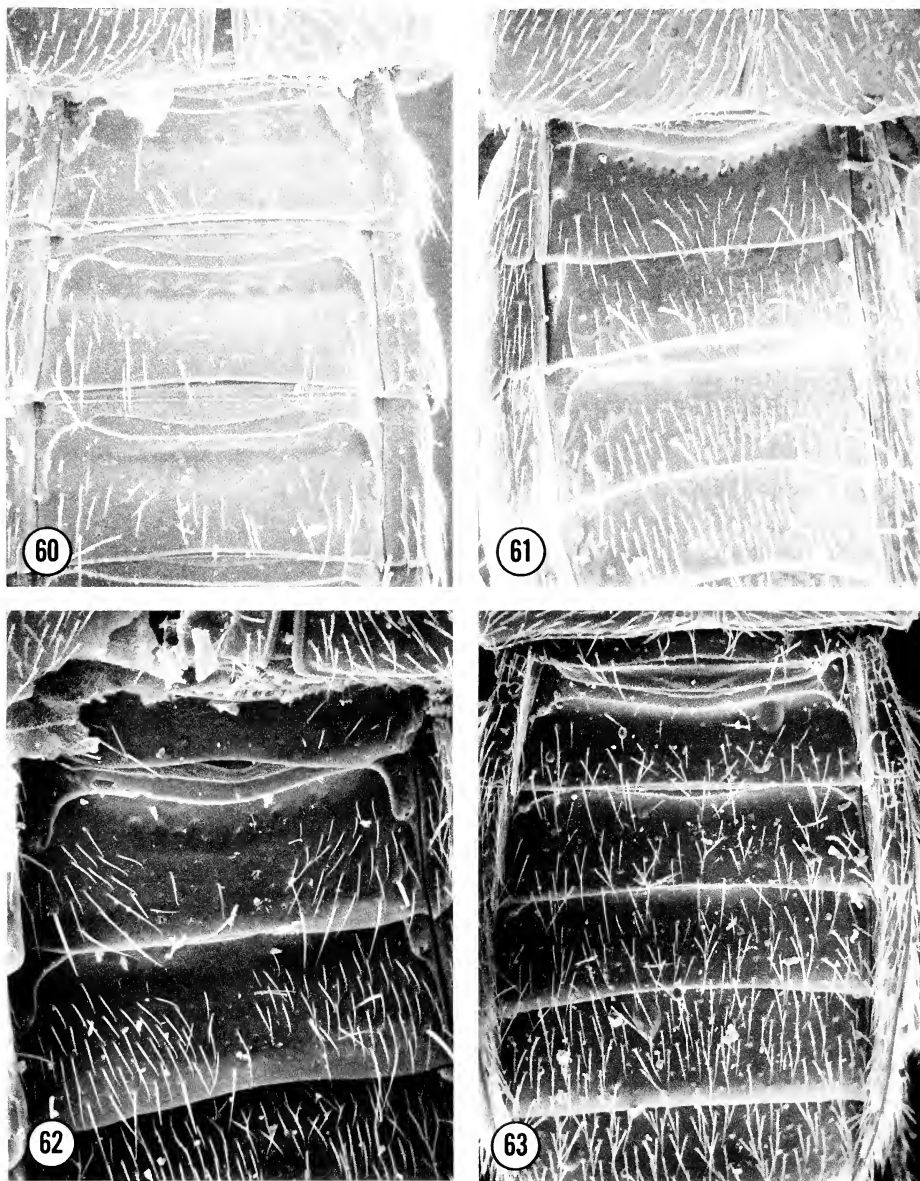
*Type-species: Staphylinus sulcatus* Paykull, fixed by subsequent designation (Blackwelder, 1952, p. 102).

Biology: Heeger, 1857, pp. 315–317; Ganglbauer, 1895, p. 254; Xamheu, 1910, p. 20; Szekessy, 1950, p. 499; Benick, 1952, p. 89.

*Diagnosis.* Adults of this genus are distinguished from those of other genera of the Falagriini by the bicarinate scutellum (Figs. 35, 44), comb of minute denticles on the apical margin of tergum VIII, delimited hypomera, deep pronotal sulcus, and uniform elytral punctation.

*Description.* Head moderate in size, about as broad as prothorax, arcuate-truncate at base, hind angles rounded. Neck narrow, about  $\frac{1}{4}$  to  $\frac{1}{5}$  as wide as head across eyes. Eyes small, slightly prominent. Labrum (Fig. 26A) moderately large, transverse. Mandibles (Fig. 26D, E) robust; right mandible with small tooth at middle of inner margin; left mandible simple. Maxilla (Fig. 26C) with galea pubescent on membranous apex; lacinia curved towards hooked apex, with rather long, curved spines on apical half of inner margin, finely setose below spines. Maxillary palpus (Fig. 26C) moderately elongate; segment 3 longer than 2, incrassate towards apex; segment 4 narrow, subuliform, at least  $\frac{1}{3}$  as long as 3. Mentum transverse, broadly emarginate on front margin. Ligula (Fig. 26B) small, narrow, distinctly split to about middle; lobes rounded at apex. Labial palpus (Fig. 26B) moderate in length; segment 2 slightly narrower and much shorter than 1; segment 3 longer and narrower than 2, distinctly dilated towards truncated apex. Antenna moderately long, slightly widened towards apex; segments 1–3 rather elongate; segment 3 as long as or shorter than 2; segments 4–10 each more transverse than preceding segment; segment 11 rather large, obtusely pointed, not as long as 9 and 10 combined. Prothorax cordiform, broadest at anterior third, strongly narrowed and converging towards base, deeply sulcate along median line, with fine, transverse and impressed line before base. Prosternum moderately short before procoxae, posterior margin with obtuse-angular process. Mesospiracular





Figs. 60-63. Basal abdominal segments of North American Falagriini, dorsal aspect. 60. *Aleodorus partitus*. 61. *Lissagria laeviuscula*. 62. *L. laticeps*. 63. *Borboropora quadriceps*.

peritremes large, quadrate, and contiguous along median line. Mesosternal process extending to about middle of mesocoxae, obtusely rounded or narrowly truncate at apex. Metasternal process obtuse, separated from mesosternal process by short isthmus in most specimens. Mesocoxae moderately separated. Hypomera delimited from pronotal disc by marginal ridge. Scutellum strongly bicarinate (Fig. 44). Elytra convex, only feebly or indistinctly sinuate at outer angles; surface minutely and uniformly punctured and pubescent, without microsculpture. Abdomen narrower than elytra at base, rather parallel or somewhat dilated at middle. Terga III–V transversely impressed at base; impressions coarsely punctate. Apical margin of tergum VIII with arcuate comb of very minute denticles.

The genus *Falagria* is widely distributed throughout the world, with the majority of species known from the north temperate regions. Two species occur in America north of Mexico.

#### KEY TO SPECIES OF *Falagria*

1. Pronotal sulcus narrow, moderately deep, interrupted near middle by a small pocket-like depression in most specimens, though sometimes indistinct in some (Fig. 35); margins and venter of abdomen towards apex without long, erect setae; spermatheca as in Figure 112 ..... *dissecta* Erichson
- Pronotal sulcus narrow and deep, not interrupted near middle by pocket-like depression; margins and venter of abdomen towards apex with long, erect setae; spermatheca as in Figure 113 ..... *sulcata* (Paykull)

#### *Falagria dissecta* Erichson

Figs. 11, 26, 35, 44, 47, 56, 91, 112; Map 9

*Falagria dissecta* Erichson, 1840, p. 49 [type locality, Pennsylvania].

*Falagria erythroptera* Melsheimer, 1846, p. 30 [type locality, Pennsylvania].

*Falagria globosa* Melsheimer, 1846, p. 30 [type locality, Pennsylvania].

*Falagria iowana* Casey, 1906, p. 247 [type locality, Iowa, Cedar Rapids].

*Falagria ithacana* Casey, 1906, p. 247 [type locality, New York, Ithaca].

*Falagria subsimilis* Casey, 1906, p. 248 [type locality, Colorado, Cañon City].

*Falagria texana* Casey, 1906, p. 248 [type locality, Texas, Austin, on the Colorado River above Columbia].

*Falagria angulata* Casey, 1906, p. 249 [type locality, Utah, St. George].

*Falagria sterilis* Casey, 1911, p. 178 [type locality, southwestern Utah].

**Diagnosis.** *Falagria dissecta* can be easily confused with the introduced species *sulcata* in external appearance, but can be distinguished by the deep pronotal sulcus which is usually interrupted near the middle by a small depression (Fig. 35), absence of long, erect setae on the margins and venter of abdomen near the apex, and the characteristic spermatheca (Fig. 112).

**Description.** Length 1.9–2.6 mm ( $N = 142$ ,  $\bar{x} = 2.17$  mm). Color pale piceo-testaceous to black or piceous-black; mouthparts, basal antennal segments, in some specimens the elytra, and legs generally paler. Habitus as in Figure 11.

Head (Fig. 11) moderate, slightly broader than long, convex, basal angles broadly rounded, broadly arcuate-truncate at base. Surface minutely, sparsely punctured and

pubescent; surface between punctures smooth and shining. Eyes equal to length of temples. Antenna moderately long and slender, reaching middle of elytra. Prothorax (Figs. 11, 35) distinctly wider than head, broadest across anterior third, strongly converging to base. Disc moderately deeply sulcate along median line except extreme apex, ending in broad, deep, rounded fovea; with small pocket-like depression interrupting sulcus near middle in most specimens (Fig. 35). Surface sparsely, finely punctured and pubescent, punctures tending to be slightly asperate; surface between punctures smooth and shining. Scutellum (Figs. 35, 44) bicarinate, consisting of two prominent, longitudinal carinae entire to apex, carinae enclosing a smooth, impressed channel. Elytra (Fig. 47) with surface densely, minutely and uniformly punctured and pubescent; punctures varying from fine to asperate among populations; surface between punctures smooth and shining. Abdomen (Fig. 56) broad at base, nearly as broad as elytra. Terga III–V broadly and transversely impressed at base; impressions with numerous, coarse, but sometimes shallow punctures. Tergal surfaces moderately densely, finely punctured and pubescent; in most specimens abdominal margins and venter at apex without long, erect setae; surface between punctures smooth and shining.

*Male.* Eighth tergite with apical margin slightly arcuate at middle, with comb of minute denticles. Eighth sternite with apical margin broadly, evenly rounded. Median lobe of aedeagus as in Figure 91A. Paramere as in Figure 91B.

*Female.* Apical margin of eighth tergite and sternite as in the male. Spermatheca as in Figure 112.

*Type material.* *Falagria dissecta* Erichson. Lectotype, here designated, with labels as follows: "Pennsylv., Zimm., Hist. Coll. Nr. 5283"/Typus/Zool. Mus. Berlin; my lectotype designation label is attached to it. Three paralectotypes have labels identical to the lectotype. One additional paralectotype has the labels: "5283"/Typus/"dissecta Er., Pennsylv. Zimm. "/Zool. Mus. Berlin. All specimens are in the Erichson collection of the Institut für Spezielle Zoologie und Zoologisches Museum, Humboldt-Universität, Berlin.

*Falagria erythroptera* Melsheimer. Holotype, with labels as follows: pink disc [=Middle States]/"Falagria erythroptera, dissecta Mels." The specimen is in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

*Falagria globosa* Melsheimer. The holotype could not be located.

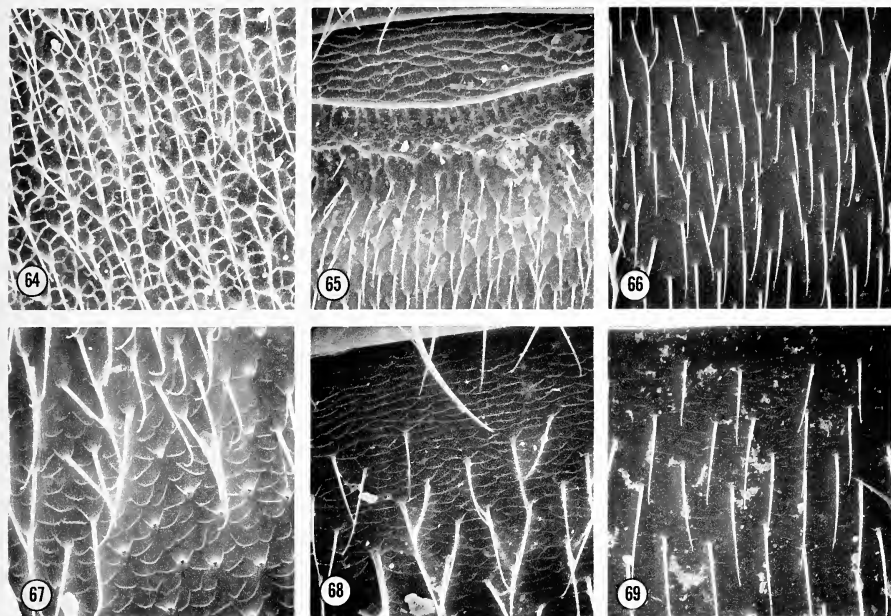
*Falagria iowana* Casey. Lectotype, here designated, with the following labels: "Ia. "/CASEY bequest 1925/Type USNM 38920/"iowana Csy."; my lectotype designation label is attached to it. In addition two paralectotypes have label data identical to that of the lectotype.

*Falagria ithacana* Casey. Holotype, with labels: "N.Y." [=Ithaca (Valley). Mr. H. H. Smith]/CASEY bequest 1925/Type USNM 38921/"ithacana Csy."

*Falagria subsimilis* Casey. Lectotype, here designated, with the labels: "Canon City, Colorado, Wickham"/CASEY bequest 1925/Type USNM 38922/"subsimilis Csy."; my lectotype designation label is attached to it. One paralectotype has the same data as the lectotype, while another has the labels: "N.M." [=Gallup, Mr. H. F. Wickham].

*Falagria texana* Casey. Lectotype, here designated, with the following labels: "Tex" [=Austin on the Colorado River above Columbia]/CASEY bequest 1925/Type USNM





Figs. 64–69. Integument of various body regions of North American Falagriini. 64. *Myrmecocephalus sculpturatus*, elytron. 65. *M. sculpturatus*, abd. segment IV. 66. *M. arizonicus*, abd. segment III. 67. *M. gatineauensis*, abd. segment VI. 68. *M. caviceps*, abd. segment VI. 69. *M. pinalicus*, abd. segment VI.

38923/“texana Csy.”; my lectotype designation label is attached to it. Three paralectotypes have labels identical to the lectotype.

*Falagria angulata* Casey. Lectotype, here designated, with labels: “St. George, Utah, July, Wickham”/CASEY bequest 1925/Type USNM 38924/“angulata Csy.”; my lectotype designation label is attached to it. In addition, three paralectotypes have labels identical to the lectotype.

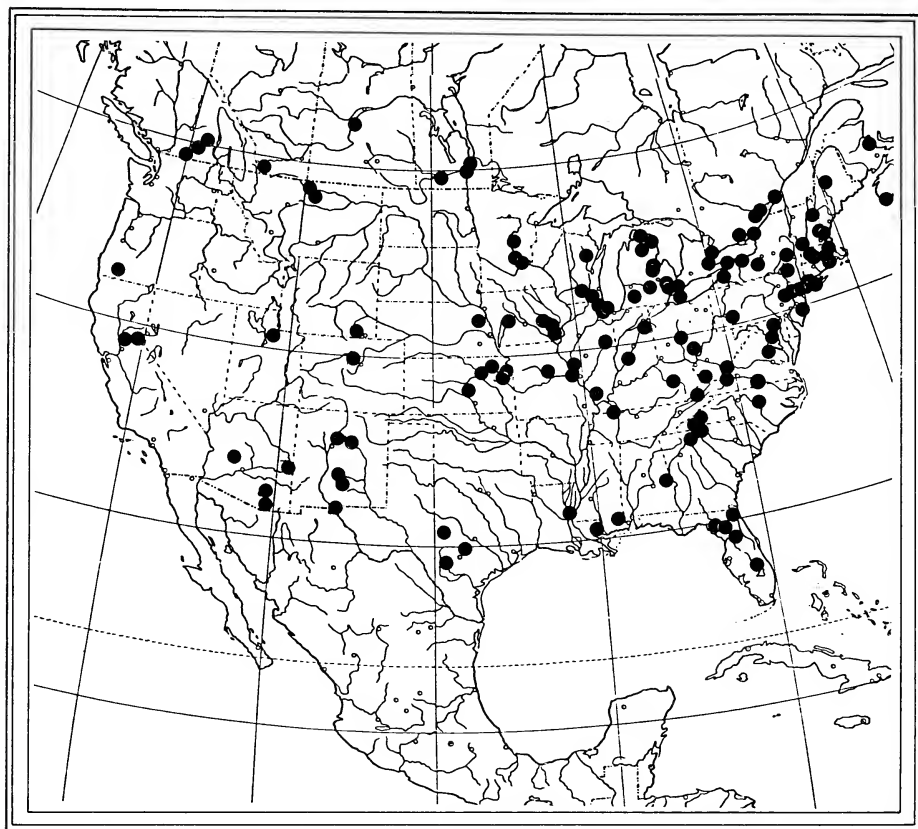
*Falagria sterilis* Casey. Holotype, with labels as follows: “Ut.”/CASEY bequest 1925/Type USNM 38925/“sterilis Csy.”

Type specimens of the above six species are in the Casey collection of the U.S. National Museum (Natural History), Washington.

*Distribution.* In America north of Mexico, *Falagria dissecta* is one of the most common species of the tribe and is transcontinental in distribution (Map 9). Specimens have been collected from January through December, with most collections made from April through September.

*Material examined.* 1,820 specimens. CANADA: *Alberta*: Highwood Pass, 7,600 ft, August (CNCI) 1; Turin, July (CNCI) 1; 16 mi S of Pincher Creek, August (CNCI) 1. *British Columbia*: Vernon, April (CNCI) 1; Summerland, December (CNCI) 1; McIntyre Rd., Oliver, 3,000 ft, May, June (CNCI) 3. *Manitoba*: Ninette, May (CNCI) 5; Pelican Lake, Ninette, May (CNCI) 5; Stonewall, April, August (CNCI) 18; Aweme



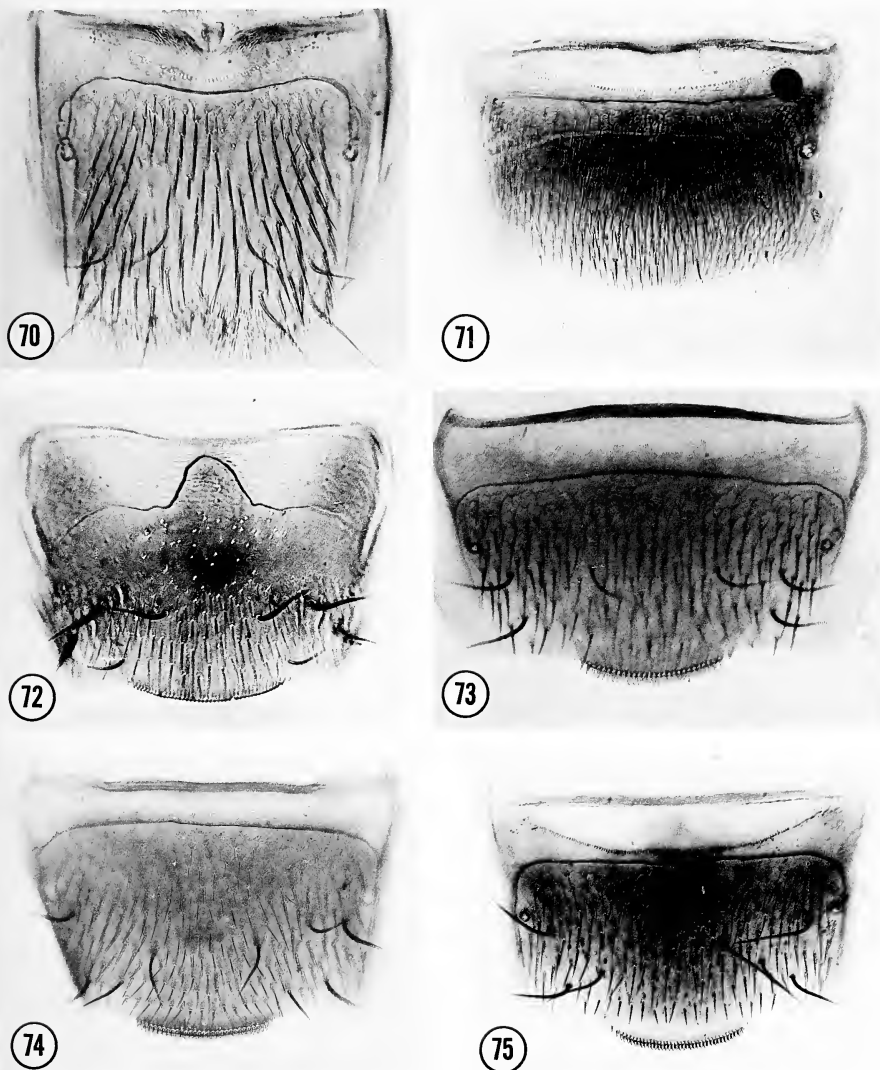


Map 9. Distribution of *Falagria dissecta*.

(USNM) 3; Spruce Woods Prov. Park, Assinibone River, June (CNCI) 1; Glenlea, 10 mi S of Winnipeg, May–June (CNCI) 2; Winnipeg, May (CNCI) 3; Bird's Hill, May (CNCI) 1; 2 mi W of Stockton, May (CNCI) 3; Manon (FMNH) 2. *New Brunswick*: Kouchibouguac N.P., June, September (CNCI) 34. *Nova Scotia*: West Light, Sable Isl., June (CNCI) 1; West end of Sable Isl., July (CNCI) 8; Sable Isl., September (CNCU) 1. *Ontario*: Ontario, June, July, August, September (CNCI) 11; Kanata, Ottawa, April (CNCI) 2; Mer Bleue, Ottawa, August–September, June–July, July–August (CNCI) 9; Marmora, June, July, August (CNCI) 11; 5 mi NW of South March, May (CNCI) 1; Pt. Pelee, June (CNCI) 1; Pelee Island, Lake Erie, August (USNM) 1; Toronto, May (CUIC) 1; Osgoode, October (CNCI) 12; Pr. Edw. Co., March, August, November (CNCI) 8; Constance Bay (CNCI) 1; Kent Co., Tilbury, May (FMNH) 2; Richmond, September (CNCI) 1; St. Lawrence Isl. Nat'l. Park, Thwartway Island, September (CNCI) 1; St. Lawrence Nat'l. Park, Grenadier Isl. W. (CNCI) 1; Ottawa, Golf Club, November (CNCI) 1. *Quebec*: Montreal, April, May, August, September, October (CUIC, MSUC, CNCI, FMNH, ZMB) 20; Montreal Isl. (FMNH) 1; 4 mi W of Masham, nr. Mud Lake, October (CNCI) 2; Knowlton, June, July

(CNCI, DENH) 2; Lac Phillipe, September (CNCI) 2; Kazabazua, August (CNCI) 1; 1 mi SW of Mont Tremblant, June (CNCI) 16; Hudson Heights, July, August, September (CNCI) 11; Mont Albert, Parc Gaspesie, July (CNCI) 1; Venise P.O., September (CNCI) 1; Bagotville, September (CNCI) 2. *Saskatchewan*: Saskatoon, May, September (CNCI) 3; Dundurn, May (CNCI) 1. UNITED STATES: *Alabama*: Auburn, March (CNCI); Opelika, March (CNCI) 4. *Arizona*: S. Rita Mts., May (USNM) 5; St. Rita Mts., Madera Cyn., August (FMNH) 1; St. Catalina Mts., Sabino Canyon, 3,000 ft, November (USNM) 1; Maricopa Co., Wickenburg, August (FMNH) 1; St. Cruz Co., Patagonia, November (FMNH) 1; Tucson, April, May (USNM) 5; Apache Nat'l. Forest, Escudilla Mt., 2,730 m, 8 mi NE of Alpine, July (CNCI) 1; Pima Co., Pantano, November (FMNH) 1. *California*: Placer Co., Lake Tahoe, Homewood, 6,200 ft, August (CNCI) 3; Yuba Co., Brown's Valley, May (UCRC) 32. *Colorado*: Kenoshe Pass, 10,000 ft, July (CASC) 1; Boulder, May (AMNH) 25. *Connecticut*: Stamford, August (FMNH) 2; state label only (USNM) 1. *District of Columbia*: Washington, March, April, July (USNM) 8. *Florida*: Okeechobee, July (FMNH) 6; Jacksonville, March (FMNH) 2; Marion Co., Lake Eaton, April (JHFC) 1; Alachua Co., San Felasco Hammock, March (JHFC) 2; Suwannee Co., 7 mi SE Branford, Santa Fe River, May (DENH) 1. *Georgia*: 5 mi W of Toccoa, September (CNCI) 5; Glynn Co., St. Simons Isl., August (JHFC) 1. *Illinois*: Urbana, Champaign, Co., June, July, August (INHS) 244; Urbana, October (INHS) 4; Urbana, July (FMNH) 1; Urbana, April (FMNH) 1; Algonquin, April, May, June (INHS, MCZC, FMNH) 16; Champaign, October (INHS) 1; Pine Hills Field Sta., Union Co., May (CNCI) 2; Cook Co., Homewood, September, October (FMNH) 172; Cook Co., Chicago, July (FMNH) 13; Cook Co., Hazelwood, September (FMNH) 10; Joliet, April (FMNH) 1; Thiedville, May, July (FMNH) 2; Chicago, April (FMNH) 1; Palos Park, May (FMNH) 1; Bowmanville, October (FMNH) 2; Glendon Park, April (FMNH) 1; Jersey Co., 1 mi W of Fieldon, April (FMNH) 4; Raccoon Grove, 2 mi S of Monee, Will Co., October (FMNH) 2; Charleston, October (INHS) 3; state label only (INHS, MSUC, WSUI) 4. *Indiana*: Bloomington, October (INHS) 13; Wells Co., 2 mi W of Bluffton, August (UCRC) 1; Tremont, June (FMNH) 1; Mineral Springs, September (FMNH) 1. *Iowa*: Iowa City (CUIC, FMNH) 4; Mt. Pleasant, March (AMNH) 2; Guthrie Center, December (LACM) 1; state label only (CUIC, FMNH) 2. *Kansas*: Lawrence, March, July, August, September, November (INHS, AMNH) 108; Manhattan, November (INHS) 3; Onaga, July (MCZC) 1; McPherson, June (MCZC) 1; Leavenworth, July (AMNH) 1; Topeka, September (FMNH) 1; Douglas Co., June (AMNH) 1; state label only (MSUC) 1. *Kentucky*: Slade, August (CNCI) 1. *Louisiana*: Concordia Co., 5 mi W of Ferriday, May (CNCI) 1; Covington, June (FMNH) 1. *Maine*: Augusta, September (DENH) 1; Kineo, June (MCZC) 1; E. Machias, June (ZMB) 1. *Maryland*: Sparrow Point, July (CASC) 1; Baltimore, July (CASC) 6; Jackson's Isl., June (USNM) 12; Mt. Lake Park, July 2,500 ft (MCZC) 2; Montgomery Co. (AMNH) 1. *Massachusetts*: S. Framingham (CNCI, FMNH, ZMB) 7; Framingham, August (CUIC) 2; Framingham, July (MCZC) 1; Framingham, August, November (MCZC, FMNH) 4; Marion (MCZC) 1; Lowell (MCZC) 2; Cambridge, January (MSUC, MCZC) 9; Wayland, October (UCSE) 3; Berlin, June (UCSE) 2; Northampton, June, August, September, October (CNCI) 8; Mer'ck River, Tyngsboro, April (MCZC) 4; Sherborn, April, November (MCZC) 2; Natick, March (MCZC) 1; Attleboro, September (MCZC) 1; Boston (MCZC) 1; Dighton, April (MCZC) 1;

Springfield, August (MCZC, USNM) 3; Lynn, July (MCZC) 2; Tatham, August (USNM) 2; Hopkinton, August (USNM) 1; Stoneham, February, March (FMNH) 3; Berkeley (FMNH) 1; Bristol Co. (FMNH) 1; Somerset, September (FMNH) 3; Fall River (FMNH) 4; state label only (FMNH, MCZC) 15. *Michigan*: Detroit, August (MSUC, USNM) 7; Alpena (INHS) 1; Alpena Co., June (MSUC) 2; Cheboygan Co., July (INHS) 9; Crawford Co., May (MSUC) 6; Oakland Co., April (MSUC, AMNH) 4; Midland Co., May (MSUC) 13; Bay Co., April, May (MSUC) 4; Wayne Co., May (MSUC) 1; Kalamazoo Co., May (MSUC) 1; Saginaw Co., September (MSUC) 1; Rose Lake Wildlife Expt. Sta., Clinton Co., April (ERHC) 2; Galesburg (MCZC, SEMC) 13; Williamston, Ingham Co., July (FMNH) 4; state label only (USNM, MSUC, DEFW) 6. *Minnesota*: Brainerd, June (CNCI) 2; Minneapolis, June, August (CNCI) 4; Elk River, August (CNCI) 6; state label only (USNM, FMNH) 9. *Missouri*: Columbia, June (CNCI) 1; state label only (USNM, FMNH, ZMB) 5; St. Louis (FMNH, ZMB) 5. *Mississippi*: Lucedale, December (CUIC) 1. *Montana*: Assinibone (USNM) 11; Bear Paw Mt., August, September (USNM) 2. *Nebraska*: West Pt., May (USNM); state label only (DEFW) 1. *New Hampshire*: Barnstead, September (CASC, CNCI) 20; W. Milton (CUIC) 1; Mt. Washington (MCZC, AMNH) 6; Mt. Washington summit, August, September (MCZC, AMNH) 4; Mt. Washington, 5–6,000 ft, July (MCZC); Farmington, August (MCZC) 3; Exeter, October (MCZC) 1; Dover, August (MCZC) 1; Three Mile Isl., June (MCZC) 3; Franconia (AMNH) 2; Strafford Co., 1 mi SW Durham, May (DENH) 4; Rockingham Co., Odiornes Pt. St. Pk., May (DENH) 1. *New Jersey*: Hampton, April, July (DENH) 2; Hopkinton, September (DENH) 1; Philipsburg, May, June, August (CASC) 5; Rahway (AMNH) 35; Avenel, May, June, August (AMNH, FMNH) 27; Snake Hill, September (AMNH) 2; Berkeley Heights, May (AMNH) 9; Fort Lee District (AMNH) 1; Westwood, July (AMNH) 1; Island Beach, Barnegal Bay (AMNH) 1; Hopatcong (AMNH) 1; Chester, July (AMNH) 12; Roselle Park, April (AMNH) 1; Monmouth Co., Sandy Hook, August (JHFC) 1; state label only (AMNH, FMNH) 8; Ocean Co., 3 mi S Tuckerton, June (DENH) 11. *New Mexico*: Sandoval Co., 15 mi NE of San Ysidro, July (CNCI) 1; Iron Creek Forest Camp, Black Range, August (FMNH) 4; Las Vegas HS, August (USNM, MCZC) 6; Las Vegas, February, April (MCZC) 2; Pecos, July (MCZC) 1; Beulah, May (MCZC) 1; Lincoln Nat'l. For., 132 mi S of Cloudcroft, 7,500 ft, July (CNCI) 1; Lincoln Co., Sierra Blanca Ski Area, 10,600 ft, July (CNCI) 1; state label only (USNM) 1. *New York*: Ithaca, August, September, October (CASC, CUIC, USNM) 15; Port Ontario, July (CASC) 1; Green Co., July (ICCM) 1; Long Island (USNM) 1; Olcott, February, April, November (CUIC) 16; Catskill Mts. (CUIC) 3; Tompkins Co., Town of Ulysses, N of Jacksonville, September (ERHC) 1; Ithaca, Tompkins Co., 1,000 ft, April (JERC) 2; Tompkins Co., Town of Caroline, April (ERHC) 1; Ithaca, Tompkins Co., September (ERHC) 1; Altamont, April (CUIC) 1; Mosholu (AMNH) 1; Ulster Co., August (AMNH) 1; Rochester, May, October, September, November (AMNH) 13; Brooklyn, November (JCCM, USNM) 6; Westchester Co. (FMNH) 2; Chataugua Co., Lake shore, Sheridan, February (CNCI) 1; Chataugua Co., April (CNCI) 2; Bronx Park, NYC (AMNH) 1; West Farms (AMNH) 1; Lake Shore, Rt. 5, April (CNCI) 1; state label only (AMNH, USNM, FMNH, INHS, MCZC) 17. *North Carolina*: Black Mt., July (CASC) 1; Glen Falls Area, 3 mi SW of Highlands, 3,200 ft, September (CNCI) 1; Clayton, May (NCSU) 1. *Ohio*: Athens, August (CNCI) 5; Columbus, July (AMNH) 1. *Oregon*: Jackson Co., 19 mi



Figs. 70–75. Abdominal tergum VIII of North American Falagriini. 70. *Cordalia obscura*. 71. *Myrmecocephalus sculpturatus*. 72. *Leptagria perexilis*. 73. *Falagrioma socorroensis*. 74. *Aleodorus bilobatus*. 75. *Lissagria laeviuscula*.

SE of Eagle Point, August (AMNH) 1. *Pennsylvania*: Easton, March, April, May, July, August, September (CASC, CNCI) 7; Pittsburgh, August (ICCM); Crisp, July (ICCM) 1; Pocono Lake, July (CASC) 1; Jeannette, July, September, October, November (CNCI, MCZC, AMNH, FMNH) 25; Chestnut Hill, June, July, August (MCZC) 2; Camp Colony, August (FMNH) 2; state label only (MCZC) 33. *Rhode*



*Island*: Barrington (MCZC) 1; state label only (MCZC, USNM) 4. *South Carolina*: Clemson, April (CNCI) 3. *Tennessee*: Ky. Lake, nr. Model, August (CNCI) 1; Sevier Co., Great Smoky Mts. Natl. Pk., 2 mi N Maddron Bald, September (CUIC) 2. *Texas*: Uvalde, April (USNM) 3; N. Braunfels, June (MCZC) 1; El Paso, November (MCZC) 3; Luling (MCZC) 1; Texas Junction, February (FMNH) 1; Cypress Mills, May (FMNH) 2; state label only (MCZC, USNM, FMNH) 3. *Utah*: Park City, June (USNM) 1; St. George, July (USNM, MCZC) 2. *Vermont*: Manchester, July (CASC) 1; Westmore, August (CNCI) 5; Bennington Co., Dorset, July (MCZC) 3; Bennington Co. (CNCI, FMNH) 2; state label only (USNM, CNCI, AMNH, FMNH) 59. *Virginia*: Stone Cr., Lee Co. (USNM) 3; Mountain Lake Biol. Stat., 2 mi N of Mountain Lake, 4,000 ft, September (CNCI) 2; Fredricksburg, July (USNM) 1; mouth of Difficult Run, August (USNM) 1; Accomack Co., Chincoteague, August (JHFC) 1. *West Virginia*: Justice, July (CUIC) 1; White Sulphur, July, August (MCZC, FMNH, ZMB) 4. *Wisconsin*: Clintonville, April, June (WSUC) 52; Madison, April, May, October (WSUC) 10; Delavan, August (FMNH) 1; state label only (CASC, FMNH) 4. *Wyoming*: Laramie (USNM) 1.

*Habitat*. Adults of this species are known to occur in a variety of habitats. Specimens at hand have been taken from malt, blacklight, and pitfall traps; from decaying vegetation, compost and animal carcasses; from under animal dung; from fungi; from debris along a beach; and from the nests or nest lining of various rodents such as beaver, marmot, and *Microtus pennsylvanicus* and *M. ochrogaster*.

*Falagria sulcata* (Paykull)

Figs. 12, 92, 113; Map 10

*Staphylinus sulcatus* Paykull, 1789, p. 32 [type locality, Sveciae].

*Falagria sulcata*; Boisduval and Lacordaire, 1836, p. 556; Erichson, 1840, p. 49; Redtenbacher, 1849, p. 651; Fairmaire and Laboulbène, 1856, p. 372; Kraatz, 1856, p. 34; Thomson, 1860, p. 297; Mulsant and Rey, 1875, p. 436; Ganglbauer, 1895, p. 255; Reitter, 1909, p. 74; Cameron, 1939, p. 243; Scheerpeltz, 1958, p. 36; Horion, 1967, p. 202; Palm, 1968, p. 77; Lohse, 1974, p. 67.

*Falagria caesa* Erichson, 1839, p. 295 [type locality, Brandenburg, Germany].

*Falagria sicula* Jekel, 1873, p. 33 [type locality, Sicily].

*Diagnosis*. Adults of this species are extremely similar to those of the closely related *F. dissecta* from which they can be distinguished by the long, erect setae of the abdominal margins and venter at the apex, absence of a pocket-like depression interrupting the pronotal sulcus near the middle, and characteristic spermatheca (Fig. 113).

*Description*. Length 2.2–3.0 mm (N = 19;  $\bar{x}$  = 2.56 mm). Color dark rufo-testaceous to piceous; mouthparts, basal antennal segments, and legs generally paler. Habitus as in Figure 12.

Head moderate in size, slightly longer than broad, broadly arcuate-truncate at base. Surface finely and somewhat moderately punctured and pubescent; surface between punctures smooth and shining. Eyes moderate, slightly prominent, equal to length of temples. Antenna moderate in length, incrassate distally, reaching to anterior half of elytra. Prothorax slightly broader than head, broadest across anterior third, strongly

converging to base. Disc narrowly and deeply sulcate along median line except at extreme apex, ending in a deep round fovea, without a pocket-like depression near middle. Surface moderately densely punctured and pubescent; punctures asperate towards sulcus in many specimens; surface between punctures smooth and polished. Scutellum strongly bicarinate, as in *dissecta*. Elytra with surface finely, relatively densely and uniformly punctured and pubescent; surface between punctures smooth and shining. Abdomen broad at base, slightly narrower at base than elytra. Terga III–V moderately deeply and transversely impressed at base; impressions with coarse, somewhat obsolete punctures. Tergal surfaces towards apex densely punctured and pubescent; towards base punctures moderately dense and slightly asperate; in most specimens abdominal margins and venter at apex with long, erect setae; surface between punctures smooth and shining.

*Male.* Eighth tergite with apical margin slightly arcuate at middle with comb of minute denticles. Eighth sternite with apical margin broadly rounded. Median lobe of aedeagus as in Figure 92A. Paramere as in Figure 92B.

*Female.* Eighth tergite and sternite with apical margin as in male. Spermatheca as in Figure 113.

*Type material.* No type material was examined for this common Palearctic species.

*Distribution.* Horion (1967, p. 202) states this species is widely distributed in the Palearctic region, from Europe, northern Africa, northern Siberia, Asia and Japan. In America north of Mexico, the species is known from northeastern and western North America (Map 10). Specimens have been collected from March through July, and in November

*Material examined.* 20 specimens. CANADA: *Alberta:* Edm.[onton], November (JHFC) 3. *Ontario:* Ottawa, August (CNCI) 1. *Quebec:* Outrement, July (CNCI) 2; Montreal (CASC) 2. UNITED STATES: ?*Illinois:* Glen View, July (FMNH) 1. *Maryland:* Baltimore, July (CASC) 1. *Massachusetts:* Arlington, April (MCZC) 1. *New Jersey:* Barnegat Bay, August (UCRC) 1; Ocean City, June, July (UCRC) 4. *New York:* Rochester, November (AMNH) 1. *Utah:* Boxelder Co., 10 mi W Brigham City, August (AMNH) 1; Utah Co., Payson, May (AMNH) 1. ?*Virginia:* Ft. Monroe (USNM) 1.

*Habitat.* Horion (1967, p. 202) claims the species is found under decaying plant material such as compost, weeds, and hay, and also from various rotting fungi. Specimens at hand from Edmonton, Alberta were collected in a haystack.

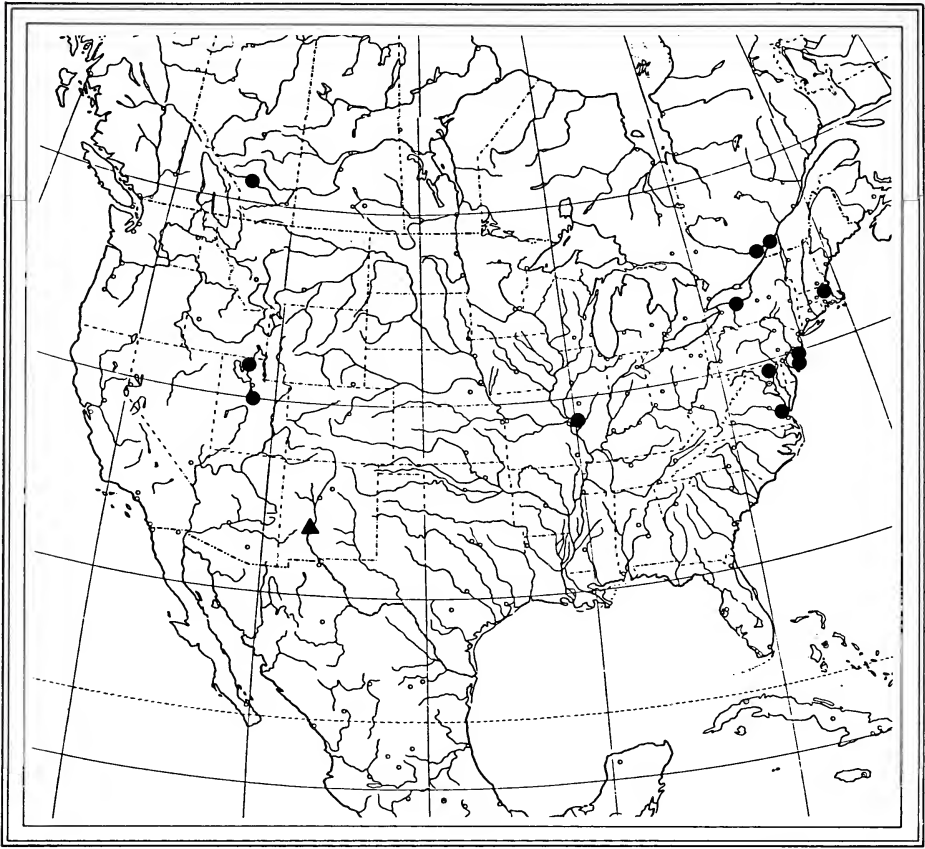
### 5. *Leptagria* Casey, Revised Status

*Leptagria* Casey, 1906, pp. 227, 249.

As synonym of *Anaulacaspis*: Fenyes, 1912, p. 24; 1920, p. 154; Bernhauer and Scheerpeltz, 1926, p. 574; Blackwelder, 1952, p. 215; SeEVERS, 1978, p. 147.

*Type-species:* *Leptagria perexilis* Casey, fixed by subsequent designation (Fenyes, 1912, p. 24).

*Diagnosis.* Adults of this genus may be separated from those of the other falagriine genera by the small body size, uniformly punctured elytra, delimited hypomera, simple, coarsely granulate, and medially channeled scutellum, and slightly arcuate apical margin of tergite VIII with a comb of minute denticles (Fig. 72).



Map 10. Distribution of *F. sulcata* (circles) and *Falagrioma socorroensis* (triangles).

*Description.* Head moderate in size, about as broad as prothorax, arcuate-truncate at base, with distinct rounded angles. Neck very narrow, about  $\frac{1}{4}$  as wide as head across eyes. Eyes well developed, prominent. Labrum (Fig. 27A) subtruncate, anterior angles broadly rounded. Mandibles (Fig. 27D, E) moderate in size, robust, slightly curved at apex; right mandible without an obvious tooth at middle of inner margin; left mandible simple, untoothed. Maxilla (Fig. 27C) with galea slightly longer than lacinia, densely pubescent on membranous apex; lacinia curved towards apex, with several stout, elongate spines at apex, densely pubescent below spines. Maxillary palpus (Fig. 27C) with segment 3 longer and broader than 2; segment 4 elongate-cylindrical. Ligula (Fig. 27B) bifid to near middle, lobes rounded at apex. Mentum (Fig. 27B) trapezoidal, broadly and shallowly emarginate along anterior margin. Labial palpus (Fig. 27B) with segment 1 elongate, broad; segment 2 short and narrower than 1; segment 3 slightly longer than 1, somewhat dilated towards apex, truncate at apex. Antenna moderately long, not strongly widened distally; segment 10 much longer than 9, slightly wider than long; segment 11 shorter than 9 and 10 combined,

apex conical and acutely pointed. Prothorax moderately small, narrowed at base. Disc deeply sulcate along median line, sulcus ending posteriorly in small, deep fovea; surface not impressed before base. Prosternum moderate in size before front coxae, posterior margin with broad cusp at middle. Mesospiracular peritremes large, quadrate and contiguous along median line. Mesosternal process wide, truncate at apex, extending to about middle of mesocoxae. Metasternal process broad, usually not separated from mesosternal process. Mesocoxae widely separated. Hypomera delimited from pronotal disc by marginal ridge. Scutellum sparsely granulose, with a smooth impressed median channel in some specimens. Elytra longer and broader than prothorax, surface minutely and uniformly punctured and pubescent, without microsculpture. Abdomen narrower at base than elytra. Terga III–V transversely impressed at base; impressions subimpunctate. Apical margin of tergum VIII with row of minute denticles (Fig. 72).

One species, *perexilis* Casey, occurs in America north of Mexico.

*Remarks.* The genus *Anaulacaspis* Ganglbauer, with the type species *Aleochara nigra* Gravenhorst, is characterized by the small body size of its members, the very fine or obsolete median pronotal sulcus, the margined hypomera, and the simple apical margin of tergum VIII. No members of *Anaulacaspis* occur in North America. The genera *Leptagria* Casey (type species: *perexilis* Csy.) and *Falagrioma* Casey (type species: *Falagria thoracica* Curtis) have been considered congeneric with *Anaulacaspis* since Fenyes (1912) and by subsequent workers including Seevers (1978). After careful examination of representatives of the type species of each genus, there is no doubt that *Leptagria* and *Falagrioma* should be recognized as distinct genera, clearly separable from *Anaulacaspis*. Characters by which they may be distinguished from *Anaulacaspis* and each other are given above and in the following paragraphs (see *Falagrioma* diagnosis).

*Leptagria perexilis* Casey

Figs. 13, 27, 36, 72, 93; Map 11

*Leptagria perexilis* Casey, 1906, p. 250 [type locality, Texas, Brownsville].

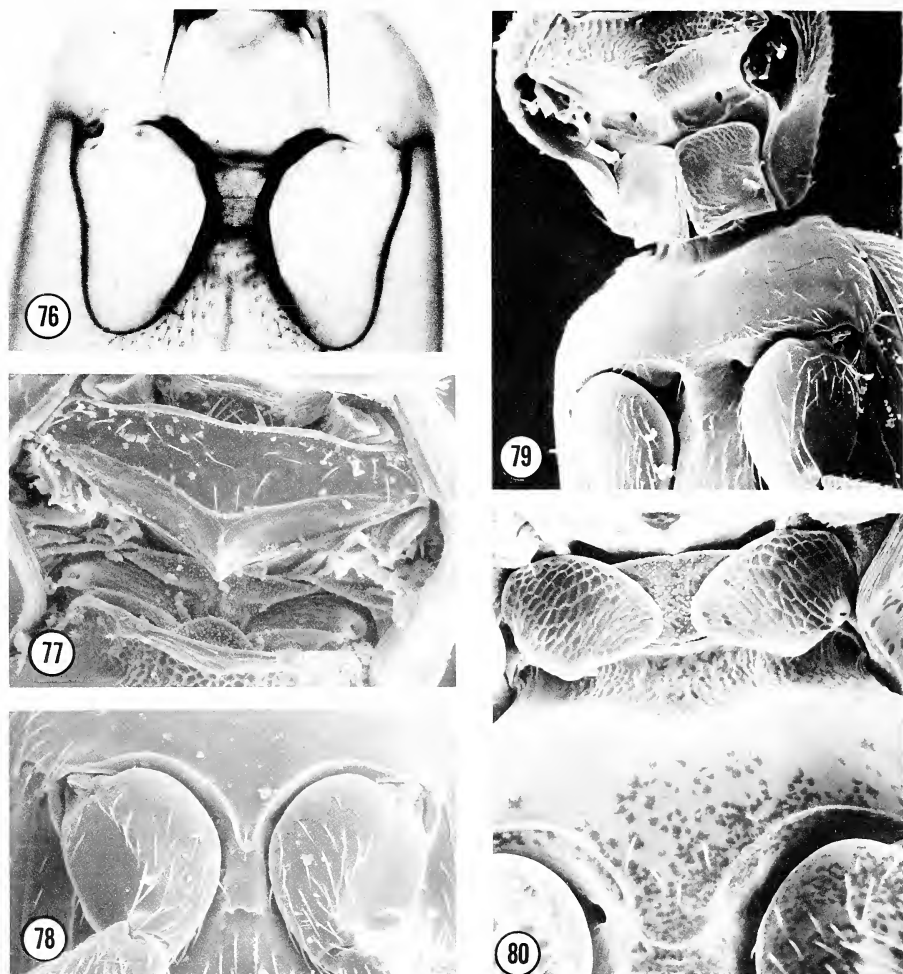
*Leptagria hudsonica* Casey, 1906, p. 251 [type locality, ?New York (Catskill Mts.)].

*Diagnosis.* Characters of the genus.

*Description.* Length 2.0–2.2 mm (N = 3;  $\bar{x}$  = 2.1 mm). Color pale to dark brownish-testaceous; mouthparts, basal antennal segments and legs slightly paler. Habitus as in Figure 13.

Head (Fig. 13) small, strongly arcuate-truncate at base; basal angles strongly rounded. Surface very sparsely and finely punctured and pubescent; surface between punctures smooth and shining. Eyes rather prominent, equal to length of temples. Antenna nearly reaching middle of elytra. Prothorax (Fig. 36) small, short, nearly equal to length of head, broadest at anterior third, strongly converging to base. Disc deeply sulcate along median line, except at extreme apex, sulcus ending in a deep, round, subbasal fovea. Surface convex, very minutely and sparsely punctured and pubescent; surface between punctures smooth and shining. Scutellum (Fig. 36) flat, finely and densely granulose and pubescent; punctures separated along median line forming smooth, narrow channel in most specimens (Fig. 36). Elytra with surface somewhat sparsely and very minutely punctured and pubescent; punctation uniform throughout;

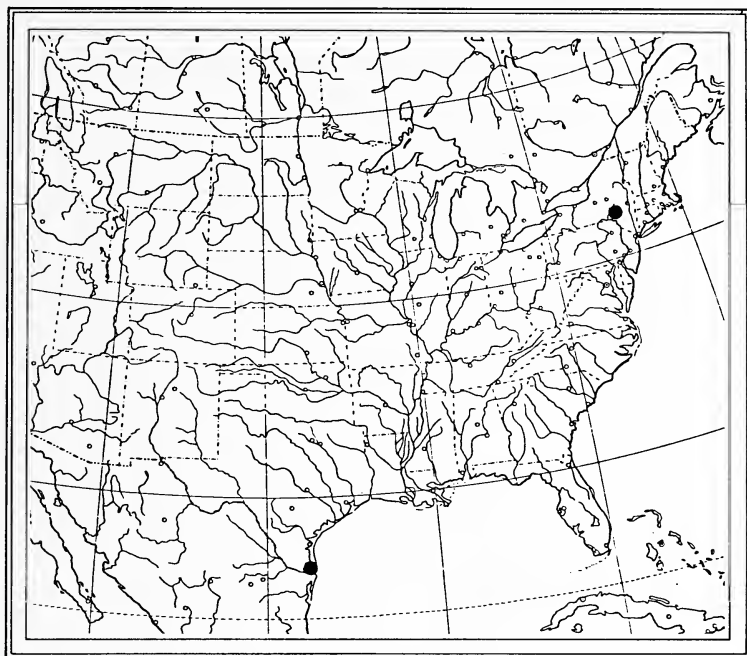




Figs. 76–80. Thoracic structures of North American Falagriini. 76. *Cordalia obscura*, meso-coxal acetabula. 77. *Falagriota occidua*, prosternum and mesospiracular peritremes. 78. *F. occidua*, meso- and metasternum. 79. *Aleodorus scutellaris*, prosternum, mesospiracular peritremes and meso- and metasternum. 80. *Lissagria laeviuscula*, mesospiracular peritremes and mesosternum.

surface between punctures smooth and polished. Abdomen broad at base, narrower than elytra. Terga III and IV strongly and deeply impressed at base; tergite V shallowly impressed at base; impression of tergite III obsolete punctured; impressions of terga IV and V impunctate. Tergal surfaces densely and very minutely punctured and pubescent; surface between punctures smooth and shining.

*Male.* Eighth tergite with apical margin slightly arcuate at middle, with comb of minute denticles (Fig. 72). Apical margin of eighth sternite broadly rounded. Median lobe of aedeagus as in Figure 93A. Paramere as in Figure 93B.



Map 11. Distribution of *Leptagria perexilis*.

*Female*. Unknown.

*Type material*. *Leptagria perexilis* Casey. Lectotype, here designated, with the following labels: "Brownsville, Texas, Wickham"/CASEY bequest 1925/Type USNM 38926/"*Leptagria perexilis* Csy."; my lectotype designation label is attached to it. Four paralectotypes have labels identical to the lectotype.

*Leptagria hudsonica* Casey. Holotype, with labels as follows: "N.Y." [=Catskill Mountains (Shokan), Mr. H. H. Smith]/CASEY bequest 1925/Type USNM 38927/"*hudsonica* Csy."

Type specimens of the above two species are in the Casey collection of the U.S. National Museum (Natural History), Washington.

*Distribution*. In America north of Mexico, *Leptagria perexilis* is known from southern Texas and southcentral New York (Map 11).

*Material examined*. 3 specimens. UNITED STATES: *Texas*: Brownsville, July (USNM) 1; San Patricio Co., Welder Wildlife Sanctuary (JHFC) 2.

*Habitat*. The habitat of this species is poorly known. Specimens at hand have been taken from cow dung and by a pond.

#### 6. *Falagrioma* Casey, Revised Status

*Falagrioma* Casey, 1906, pp. 226, 230.

As synonym of *Anaulacaspis* Ganglbauer: Fenyés, 1912, pp. 24, 27; 1920, p. 154; Bernhauer and Scheerpeltz, 1926, p. 574; Blackwelder, 1952, p. 164; Moore and Legner, 1975, p. 414; Seevers, 1978, p. 147.

As subgenus of *Falagria*: Tottenham, 1957, p. 90.

Variant spelling: *Falagrionia* Tottenham, 1949, p. 387.

*Type-species: Falagria thoracica* Curtis, fixed by monotypy (Casey, 1906, p. 230).

*Anaulacaspis* sensu Jarrige, 1946, p. 252; Horion, 1951, p. 169; 1967, p. 203; Lohse, 1974, p. 66; Last, 1979, p. 233.

*Anaulacaspis* auctorum (ex parte): Bernhauer and Scheerpeltz, 1926, pp. 574, 578; Scheerpeltz, 1934, pp. 1573, 1574; Cameron, 1939, p. 243.

*Falagria* sensu Kistner, 1971, p. 155.

*Falagria* auctorum (ex parte): Fowler, 1898, p. 748; Everts, 1898, p. 231; Portevin, 1929, p. 294; Redtenbacher, 1874, p. 129; Rapp, 1933, p. 402.

Biology: Johnson and Halbert, 1902, p. 633; Schaufuss, 1916, p. 226; Jarrige, 1946, p. 252; Rapp, 1933, p. 403; Kistner, 1971, pp. 158, 162–164.

*Diagnosis.* Adults of this genus are distinguished from those of other falagriine genera by the moderately, deeply sulcate pronotum; delimited hypomera; simple, unmodified and granulose scutellum; area of dense and coarse punctation of the elytra near the scutellum; and arcuate comb of denticles on the apical margin of tergum VIII.

*Description.* Head arcuate-truncate at base, with rounded hind angles. Neck slender, more than  $\frac{1}{4}$  as wide as head across eyes. Eyes rather small, not prominent. Labrum (Fig. 28A) moderate, transverse, front angles broadly rounded. Mandibles (Fig. 28D, E) robust, prominent. Maxilla (Fig. 28C) with galea densely setose on membranous apex; lacinia curved at apex, with rather long and curved spines on apical half of inner margin, finely setose below spines. Maxillary palpus (Fig. 28C) moderately elongate; segment 1 short; segment 2 elongate, dilated at apex; segment 3 longer than 2, incassate at apex; segment 4 narrow, subuliform,  $\frac{1}{3}$  as long as 3. Mentum (Fig. 28B) large, transverse, broadly emarginate on front margin. Ligula (Fig. 28B) small, narrow, and bifid to middle, lobes rounded at apex. Labial palpus (Fig. 28B) elongate; segment 1 long, broad; segment 2 narrower and much shorter,  $\frac{1}{3}$  as long as 1; segment 3 longer and slightly narrower than 2, distinctly widened towards truncated apex. Antenna stout; terminal segments strongly transverse and compact; segment 11 not as long as 9 and 10 combined. Prothorax short, slightly longer than broad, moderately to strongly narrowed towards base. Disc moderately, deeply sulcate except at extreme apex, sulcus ending basally in a small, rounded or slightly transverse fovea. Prosternum moderately large in front of procoxae, flat, posterior margin cusped at middle. Mesospiracular peritremes large, quadrate, contiguous or slightly overlapping along median line. Mesosternal process free, rather long, obtusely rounded and extending to middle of mesocoxae, separated from metasternal process by a short, depressed isthmus. Mesocoxae moderately separated. Hypomera short, dilated at middle, delimited from disc by fine marginal ridge (Fig. 41). Scutellum flat, unmodified, densely punctured. Elytra longer and broader than prothorax, evenly convex, surface densely punctured towards scutellum (Fig. 48), without microsculpture. Abdomen moderately broad at base. Impressions of terga III–V narrow, deep, and acutely impressed, coarsely and sparsely punctured. Apical margin of tergum VIII with arcuate comb of small denticles.

One species, *socorroensis* n. sp., occurs in America north of Mexico.

**Falagrioma socorroensis**, new species

Figs. 14, 73, 113, Map 10

*Diagnosis.* Characters of the genus.

*Description.* Length 2.8 mm. Color rufo-brunneous; mouthparts, basal antennal segments 1 or 2 and legs paler. Habitus as in Figure 14.

Head moderately small, as broad as prothorax, slightly longer than broad, sides slightly arcuate, base broadly arcuate-truncate, hind angles rounded. Surface between and behind antennal insertions broadly impressed; frons moderately coarsely punctured and pubescent; surface between punctures smooth and polished. Eyes not prominent, equal to length of temples. Antenna moderately long, reaching middle of elytra. Prothorax slightly longer than broad, gradually narrowed to base, longer than head, broadest across anterior third; anterior angles broadly rounded, lateral margins converging towards base, posterior margin slightly arcuate. Disc deeply sulcate along median line except at apex, sulcus ending in a deep, slightly transverse fovea. Surface finely and densely punctured and pubescent, punctures more coarse and dense towards sulcus; surface between punctures smooth and polished. Scutellum nearly convex, coarsely and densely punctured and pubescent. Elytra with surface moderately and finely punctured and pubescent, punctures more coarse and dense towards scutellum (similar to that of Fig. 48); surface between punctures smooth and shining. Abdomen moderately broad at base, gradually narrowed to apex. Terga III–V broadly, transversely impressed at base; impressions densely granulate; impression of tergum III also shallowly foveate. Tergal surfaces towards apex finely and densely punctured and pubescent, punctures more asperate and coarse towards base; surface between punctures smooth and polished.

*Male.* Unknown.

*Female.* Eighth tergite with apical margin broadly arcuate at middle, with comb of denticles (Fig. 73). Apical margin of eighth sternite broadly and evenly rounded. Spermatheca as in Figure 114.

*Type material.* Holotype, female, with labels: Socorro Co., N.M., Aug '94, Snow/ Det. by G. H. Horn/HOLOTYPE *Falagrioma socorroensis*, E. R. Hoebeke 1981. The type is deposited in the Snow Entomological Museum, University of Kansas, Lawrence.

*Distribution.* *Falagrioma socorroensis* is known only from the type locality, Socorro County, New Mexico (Map 10).

*Habitat.* Details of the biology and habitat of this species are unknown.

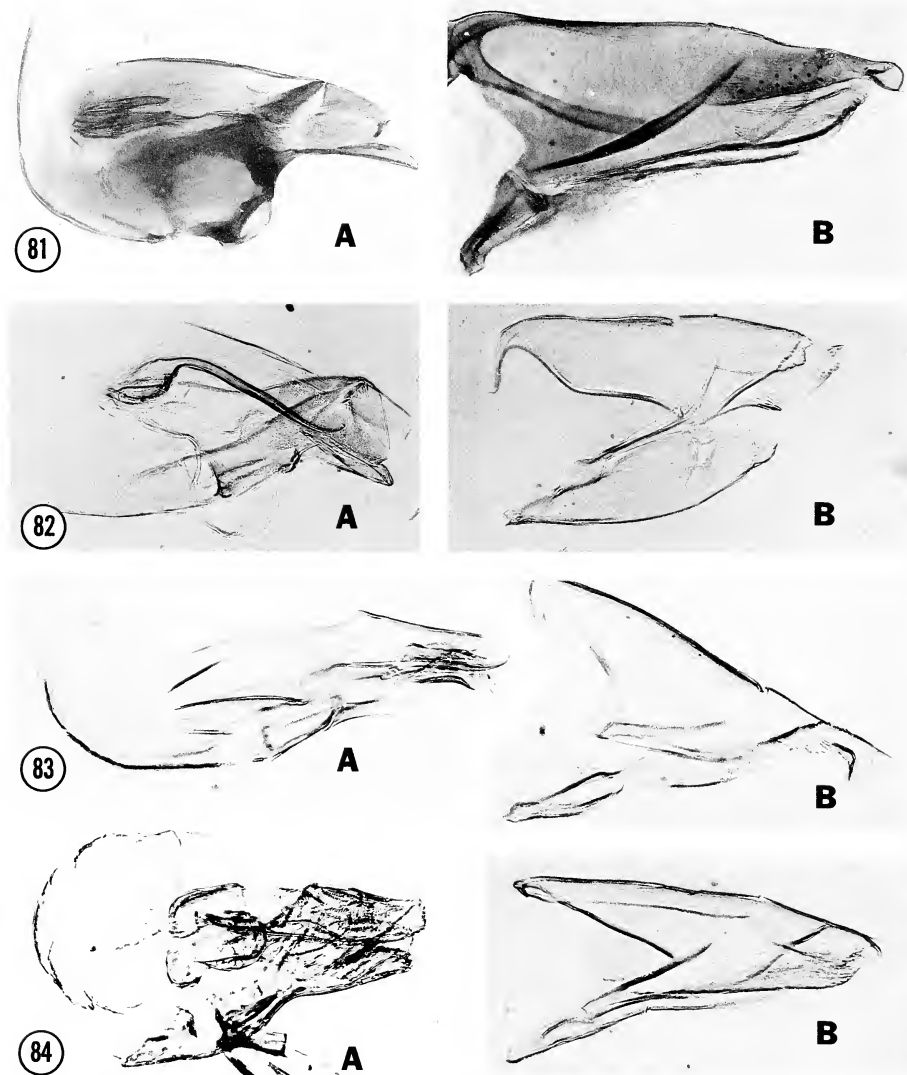
*Etymology.* *Socorroensis* is an adjective derived from the place name Socorro County (New Mexico), and refers to the origin of the type specimen.

### 7. *Aleodorus* Say

*Aleodorus* Say, 1830, p. 60; 1839, p. 157; Fenyès, 1912, pp. 20, 22, 25; Leng, 1920, p. 124; Bernhauer and Scheerpeltz, 1926, p. 571; Bradley, 1930; pp. 85, 313; Scheerpeltz, 1934, p. 1568; Blackwelder, 1944, p. 158; 1952, p. 45; Arnett, 1968, p. 288; Moore and Legner, 1975, p. 336; Seevers, 1978, pp. 54, 145.

Variant spelling: *Aleoderus* Lynch, 1884, p. 29.





Figs. 81–84. Male genitalia of North American Falagriini [A, median lobe, lateral aspect; B, paramere]. 81. *Cordalia obscura*. 82. *Falagriota occidua*. 83. *Myrmecocephalus cingulatus*. 84. *M. concinnus*.

*Type-species: Aleochara bilobata* Say, fixed by original designation and monotypy (Say, 1830, p. 60).

*Chitalia* Sharp, 1883, p. 235; Casey, 1906, pp. 225, 232; Blatchley, 1910, pp. 345, 346; Fenyès, 1912, p. 22; 1918, p. 18; 1920, p. 148; Notman, 1920, p. 731; Blackwelder, 1952, p. 45.

*Type-species: Chitalia crenata* Sharp, fixed by subsequent designation (Fenyés, 1912, p. 22).

*Diagnosis.* Adults of this genus are distinguishable from those of other Falagriini by the mesosternum, which is in a plane ventral to the metasternum (Fig. 78), the short, acute mesosternal process (Fig. 78), and highly convoluted flagellum of the internal sac of the median lobe (Figs. 94–97).

*Description.* Head arcuate-truncate at base, slightly narrower than widest portion of prothorax. Neck very slender, approximately ¼ as wide as head across eyes. Eyes moderately large to small. Labrum (Fig. 29A) short, transverse; anterior angles rounded; anterior margin subtruncate. Mandibles (Fig. 29D, E) moderate in size, apex curved; right mandible with inconspicuous projection at middle of inner margin; left mandible simple. Maxilla (Fig. 29C) with galea shorter than lacinia, densely pubescent on membranous apex; lacinia curved towards hooked apex with spines on apical half of inner margin, densely pubescent on basal half. Maxillary palpus (Fig. 29C) elongate; segment 1 minute; segment 2 elongate, much longer than 1; segment 3 slightly longer than 2; segment 4 very narrow, aciculate. Mentum transverse, slightly emarginate on front margin. Ligula (Fig. 29B) small, bifid; lobes rounded. Labial palpus (Fig. 29B) small; segment 1 stout and long; segment 2 shorter and narrower than 1; apical segment conical, truncate at apex. Antenna very stout; segments 1–3 long, nearly subequal in length; segments 4–10 gradually increasing in width, feebly transverse, densely pubescent; apical segment short, conical, shorter than segments 9 and 10 combined. Pronotum strongly narrowed at base, lateral margins broadly constricted behind widely dilated anterior portion, anterior margin broadly produced, posterior margin truncate to broadly concave. Disc strongly sulcate along median line. Prosternum moderately long, broadly transverse, all but anterior margin and sides concealed by procoxae, hind margin strongly, acutely cusped at middle. Mesospiracular peritremes large, quadrate, contiguous along median line. Mesosternal process abbreviated and broad, extending short distance between mesocoxae. Metasternum smooth, impunctate; metasternal process long and broad, transversely convex. Mesocoxae widely separated. Hypomera not delimited from disc by marginal ridge. Scutellum large, triangular, with coarse, asperate punctures, punctures parted along median line by a narrow to broad, smooth impression in most specimens. Elytra slightly longer than or equal to pronotal length; lateral margins subparallel, slightly arcuate posteriorly; surface evenly convex, finely and closely punctured and pubescent; area of dense and coarse punctation near scutellum. Abdomen elongate, subparallel, gradually tapering to apex, narrower at base than elytra. Terga III–V strongly and transversely impressed at base; impressions coarsely to sparsely punctured or foveate. Apex of tergum VIII with an arcuate row of small denticles.

Members of the genus *Aleodorus* are restricted to the Western Hemisphere. Four species occur in America north of Mexico.

KEY TO SPECIES OF *Aleodorus*

- 1. Foveae of basal abdominal impressions large and contiguous (Fig. 57); size large, most specimens greater than 3.0 mm ..... 2
- Foveae of basal abdominal impressions coarse and clearly separated (Fig. 60); size small, most specimens under 2.5 mm ..... *partitus* (LeConte)

2. Foveae of abdominal impressions shallow, basins minutely punctulate (appearing finely granulose at high magnification) (Fig. 59) ..... *intricatus* (Casey)
- Foveae of abdominal impressions deeper, basins scarcely punctulate (appearing smooth or nearly so at high magnification) (Fig. 58) ..... 3
3. Scutellum with broad, smooth, and impressed median channel (Fig. 37) ..... *scutellaris* (LeConte)
- Scutellum without broad, median channel (though some specimens with a faint, narrow channel) ..... *bilobatus* (Say)

*Aleodorus partitus* (LeConte)

Figs. 15, 60, 94, 115; Map 12

*Falagria partita* LeConte, 1866, p. 371 [type locality, Louisiana].

*Chitalia floridana* Casey, 1906, p. 237 [type locality, Florida].

*Chitalia novella* Casey, 1911, p. 176 [type locality, Texas, Austin, on the Colorado River above Columbia].

*Aleodorus partita*; Bernhauer and Scheerpeltz, 1926, p. 572.

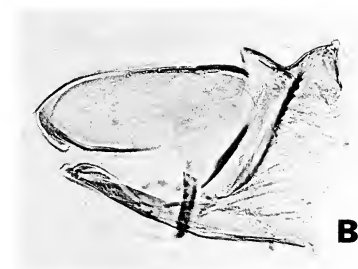
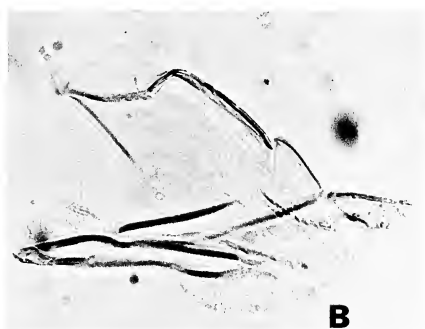
*Aleodorus partitus*; Notman, 1920, p. 730; Scheerpeltz, 1934, p. 1568.

**Diagnosis.** Adults of *Aleodorus partitus* are the smallest of the genus in America north of Mexico. In addition to small size, they may be separated from others of the genus by the few, coarse, well-separated foveae of the basal impression of tergum III (Fig. 60).

**Description.** Length 2.0–2.3 mm (N = 13;  $\bar{x}$  = 2.2 mm). Color uniformly light to dark rufo-testaceous; mouthparts, antennae and legs pale, head and abdomen occasionally dark. Habitus as in Figure 15.

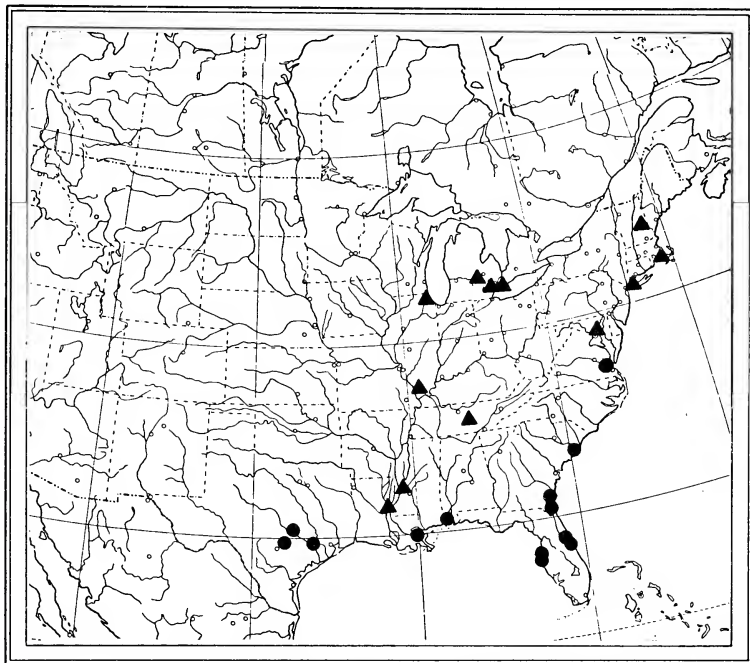
Head (Fig. 15) relatively large, longer than broad, not quite as broad as prothorax, arcuate-truncate at base; basal angles broadly rounded. Surface minutely and sparsely punctured and pubescent; surface between punctures smooth and polished. Eyes equal to length of temples. Antenna stout, reaching to basal  $\frac{1}{3}$  of elytra or slightly beyond. Prothorax (Fig. 15) as wide as long, narrower than head, broadest at anterior third, strongly narrowing and converging to base; lateral margins slightly sinuate posteriorly; posterior margin nearly straight or slightly arcuate. Disc strongly sulcate along median line except extreme apex, sulcus ending in subbasal fovea; surface sometimes broadly impressed and flattened adjacent to sulcus. Surface minutely and sparsely punctured and pubescent; surface between punctures smooth and shining. Scutellum flat, sparsely and coarsely punctured; punctures asperate, with a smooth impressed channel along median line in some specimens. Elytra with surface minutely, sparsely and uniformly punctured and pubescent, except area of dense and coarse punctation near scutellum. Abdomen broad at base, narrower than elytra. Terga III–V moderately and transversely impressed at base; impressions of terga III and IV with several coarse and well-separated foveae (Fig. 60); impression of tergum V occasionally with fewer and subobsolete punctures (sometimes absent altogether). Tergal surfaces minutely and sparsely punctured and sparsely pubescent; punctures tending to be fine and partly asperate towards base; surface between punctures smooth, polished.

**Male.** Eighth tergite with apical margin broadly arcuate at middle, with comb of minute denticles. Eighth sternite with apical margin broadly rounded. Median lobe of aedeagus as in Figure 94A. Paramere as in Figure 94B.



Figs. 85–88. Male genitalia of North American Falagriini. 85. *Myrmecocephalus gracilis*. 86. *M. sculpturatus*. 87. *M. arizonicus*. 88. *M. gatineauensis*.





Map 12. Distribution of *Aleodorus partitus* (circles) and *A. scutellaris* (triangles).

*Female.* Eighth tergite and sternite with apical margin as in the male. Spermatheca as in Figure 115.

*Type material.* *Falagria partita* LeConte. Lectotype, here designated, with the following labels: "LS"(?)/partita 2/partita 3; my lectotype designation label is attached to it. This specimen is mounted on a paper point (point marked with red) and on the same pin with another point-mounted paralectotype. A third paralectotype in the LeConte collection is labeled: "Fla.,"/Type 6242. This specimen was not selected as the lectotype because the abdomen is missing. In addition, I have examined another specimen (paralectotype) in the Horn collection labeled as *partita*.

*Chitalia floridana* Casey. Lectotype, here designated, with labels as follows: "aulover, II ch 25, Fla.,"/CASEY bequest 1925/Type USNM 38909/"floridana Csy."; my lectotype designation label is attached to it. One paralectotype is labeled: "Enterprise, Fla.," while another is with labels: "Fla." [=Enterprise]. All specimens are in the U.S. National Museum (Natural History), Washington.

*Chitalia novella* Casey. Holotype, with labels as follows: "Tex" [=Austin on the Colorado River above Columbia.]/CASEY bequest 1925/Type USNM 38908/"novella Csy." The specimen is in the collection of the U.S. National Museum (Natural History), Washington.

*Distribution.* *Aleodorus partitus* is known from Virginia south to Florida and west to Texas (Map 12). Specimens have been collected from February through October.

*Material examined.* 43 specimens. UNITED STATES: *Alabama:* Mobile (FMNH)

3. *Florida*: Dunedin, March, April (CUIC, MCZC) 8; St. Petersburg, March (MCZC) 2; Fernandina Beach, March (MCZC) 1; Enterprise, May, June (AMNH, MCZC) 3; Sand Point, February, April (USNM) 2; Titusville (AMNH) 1; state label only (AMNH) 3. *Georgia*: St. Simons Island, July (MCZC) 1. *Louisiana*: New Orleans, March (USNM) 1; state label only (MCZC) 5. *South Carolina*: Charleston Co., Climax, October (JHFC) 1. *Texas*: New Braunfels, June (MCZC) 1; Columbus, June, July (USNM) 7; state label only (USNM, MCZC) 3. *Virginia*: Ft. Monroe (USNM) 1.

*Habitat*. Few details are available regarding biology or habitat of this species. Two Texas specimens were collected from the nest of a beaver.

*Aleodorus intricatus* (Casey)

Figs. 16, 45, 59, 95, 116; Map 13

*Chitalia intricata* Casey, 1906, p. 234 [type locality, New Mexico, Gallup].

*Aleodorus intricata*; Bernhauer and Scheerpeltz, 1926, p. 572.

*Aleodorus intricatus*; Scheerpeltz, 1934, p. 1568; Moore and Legner, 1975, p. 336.

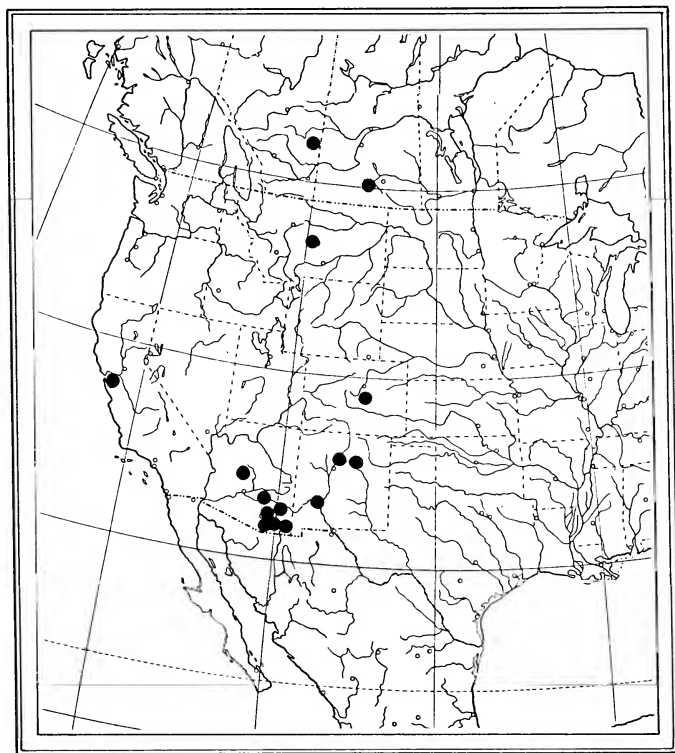
*Diagnosis*. Adults are very similar externally to those of *bilobatus* and *scutellaris*, but with an allopatric western North American distribution (Map 13), and differing by the minutely granulose basins of the foveae of abdominal impressions III–V (Fig. 59).

*Description*. Length 3.1–4.1 mm ( $N = 92$ ;  $\bar{x} = 3.52$  mm). Color uniformly light to dark brownish-testaceous; in some specimens head darker and abdomen beyond third segment piceous; mouthparts, basal 2 antennal segments and legs paler. Habitus as in Figure 16.

Head (Fig. 16) slightly longer than broad, not as broad as prothorax, slightly impressed on median line of occiput, arcuate-truncate at base, basal angles broadly rounded. Surface sparsely, finely punctured and pubescent; surface between punctures smooth and polished. Eyes equal to length of temples. Antenna similar in structure to that of *bilobatus*. Prothorax (Fig. 16) nearly as wide as long, broadest anteriorly, narrowing and converging in basal half; lateral margins strongly sinuate; posterior margin nearly straight. Disc deeply sulcate along median line except extreme apex, sulcus ending in a subbasal fovea. Surface finely, sparsely punctured and pubescent, punctures somewhat asperate, more coarse and dense towards sulcus; surface between punctures smooth and shining. Scutellum (Fig. 45) coarsely punctured, with a slightly narrow but distinct, smooth channel along median line, complete to apex in some specimens. Elytra with surface minutely and sparsely punctured and pubescent, punctures tending to be more dense and coarse towards scutellum; surface between punctures smooth and polished. Abdomen broad at base, narrower than elytra. Terga III–V strongly and transversely impressed at base; impressions strongly foveate, basins densely and minutely punctulate (Fig. 59). Surface finely, sparsely punctured and pubescent towards apex; punctures more asperate and coarse at base; surface between punctures smooth and polished.

*Male*. Eighth tergite with apical margin broadly arcuate at middle, with comb of denticles. Eighth sternite with apical margin broadly, evenly rounded. Median lobe of aedeagus as in Figure 95A. Paramere as in Figure 95B.

*Female*. Eighth tergite and sternite with apical margin as in the male. Spermatheca as in Figure 116.



Map 13. Distribution of *A. intricatus*.

*Type material.* Lectotype, here designated, with labels as follows: "N.M." [=Galup, Mr. H. F. Wickham]/CASEY bequest 1925/Type USNM 38907/"intricata Csy."; my lectotype designation label is attached to it. One paralectotype has labels identical to the lectotype. Both specimens are in the U.S. National Museum (Natural History), Washington.

*Distribution.* *Aleodorus intricatus* occurs at moderately high elevations in western North America, from southern Alberta and Saskatchewan south to southern Arizona and New Mexico, and west to California (Map 13). Specimens have been collected from March through November, with most collections made from May through July.

*Material examined.* 237 specimens. CANADA: *Alberta*: Gooseberry Lk., October (JHFC) 1. *Saskatchewan*: Willows, June (CNCI) 5; Willows, 49°37', 105°52', June (CNCI) 1. UNITED STATES: *Arizona*: Sierra Vista, Cochise Co., March, April, May, October, November (CNCI) 18; Ramsey Canyon, 5,200 ft, 15 mi S of Sierra Vista, August, September (CNCI) 31; Pinery Canyon, Chiricahua Mts., 6,600 ft, June (CNCI) 3; Miller Canyon, Huachuca Mts., 6,500–7,000 ft, August (CNCI) 1; Madera Canyon, Santa Rita Mts., May (AMNH) 8; Ash Spring, Chiricahua Mts., May (AMNH); Ramsey Canyon, Huachuca Mts., 6,500–7,000 ft, May (AMNH) 20; Green House Canyon, 3 mi S of SWRS, Chiricahua Mts., 5,500 ft, May (AMNH) 21; E. Turkey

Creek, Chiricahua Mts., 6,000 ft, May (AMNH) 15; 5 mi W of Portal, 5,400 ft, April (AMNH) 5; Pinal Mts., Gila Co. (MCZC) 1; S. Rita Mts., May, June (USNM) 10; Prescott (USNM) 1; Chiricahua Mts., May, June, July (USNM) 36; Mt. Lemmon, 9,000 ft, May (UCRC) 1; Pinaleno Mts., Wet Canyon, 6,000 ft, July (CNCI) 3; 7 mi W of East Turkey Creek, July (CNCI) 1; 5 mi W of Portal, 5,500 ft (CNCI) 1; Cochise Co., Portal, 5,000 ft, July (CNCI) 2; Pinal Co., Oracle, 4,500 ft, May (CNCI) 1; Santa Rita Mts., Madera Canyon, 5,500 ft, August (CNCI) 1; Ramsey Canyon, Cochise Co., 5,200 ft, July (CNCI) 1; Copper Canyon, Huachuca Mts., June (FMNH) 1; Graham Mts., Wet Canyon, September (FMNH) 1; Sunnyside, Cochise Co., June (FMNH) 1; Santa Rita Mts., Madera Canyon, November (FMNH) 2; Wet Canyon Camp Gr., Graham Mts., 6,000 ft, September (FMNH) 2; state label only (MCZC) 1. *California*: Alameda Co., September (FMNH) 1. *Colorado*: Colorado Springs, 6,000–7,000 ft, June (MCZC) 1. *Montana*: state label only (INHS) 1. *New Mexico*: Las Vegas, August (MCZC, USNM) 6; Jemez Mts., April (CASC) 7; Sierra Co., Emory Pass, July (CNCI) 1; [El] Porvenir (FMNH) 1.

*Habitat*. Little is known about the biology and habitat of this species. Specimens at hand have been taken from leaf litter, and from along a stream shore.

*Aleodorus scutellaris* (LeConte),

**Revised Status, New Combination**

Figs. 17, 37, 57, 58, 79, 96, 117; Map 12

*Falagria scutellaris* LeConte, 1866, p. 370 [type locality, New York, Coney Island].

*Chitalia granulosa* Casey, 1906, p. 235 [type locality, Mississippi, Vicksburg]. **New**

**Synonym.**

*Chitalia illustris* Casey, 1906, p. 235 [type locality, Mississippi, Vicksburg]. **New**

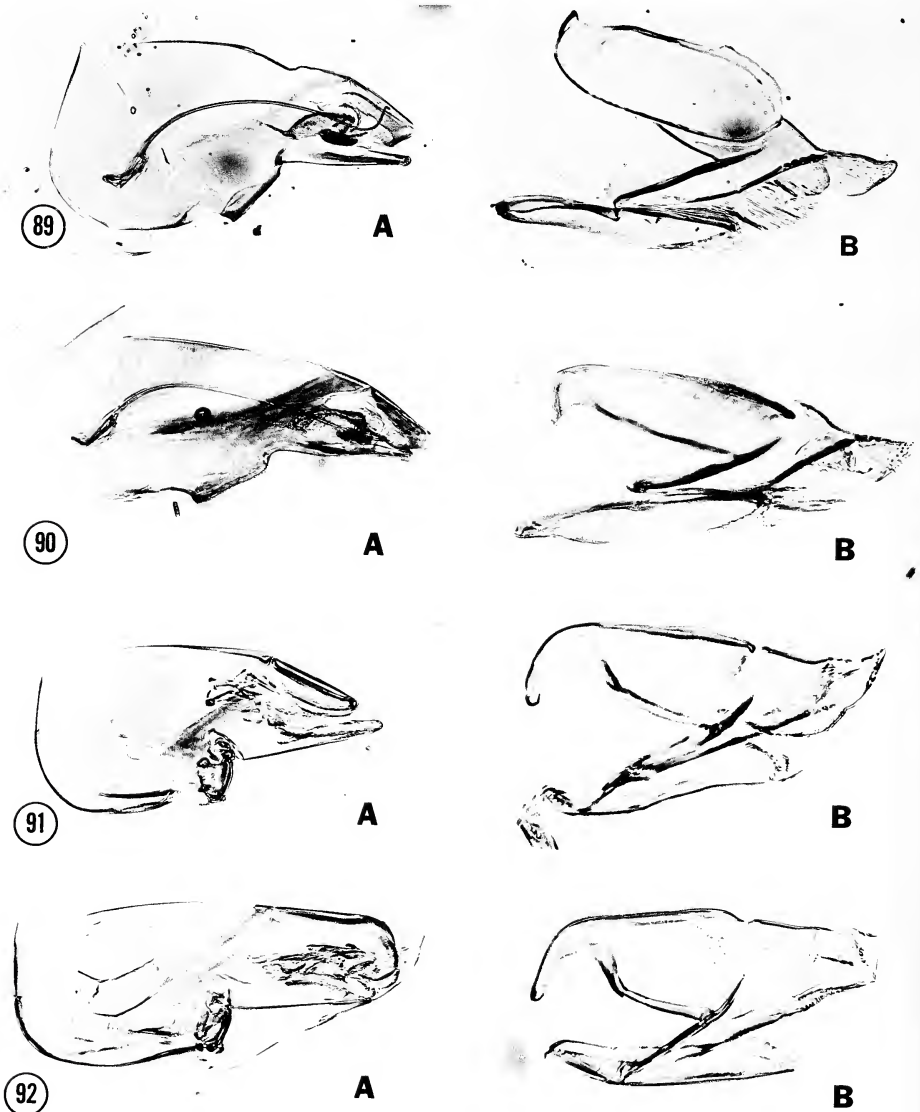
**Synonym.**

*Diagnosis*. This species is extremely similar to *bilobatus* in appearance but differs by the broad, smooth, impressed channel of the scutellum (Fig. 37), and presence of a series of the fine ridges on the inner surface of the paramere of the male genitalia (Fig. 96B).

*Description*. Length 2.9–3.6 mm ( $N = 38$ ;  $\bar{x} = 3.25$  mm). Color light to dark ferrugineous, or piceous; mouthparts, basal antennal segments and legs paler in most specimens. Habitus as in Figure 17.

Head (Fig. 17) slightly longer than wide, nearly as wide as prothorax, sides evenly arcuate, arcuate-truncate at base, basal angles broadly rounded. Punctuation and pubescence fine and moderately dense on dorsum; surface between punctures smooth and shining. Eyes equal to or longer than temples. Antenna moderately stout, elongate, reaching middle of elytra. Prothorax (Figs. 17, 37) about as wide as head, broadest across anterior third, narrowing and converging strongly towards base, lateral margins slightly sinuate. Disc strongly sulcate along median line except at extreme apex, sulcus ending in a broad, subbasal fovea. Surface densely, coarsely punctured, and moderately densely pubescent; surface between punctures smooth and shining. Scutellum (Fig. 37) flat or slightly convex, densely punctured, with a broad, smooth, and slightly impressed, median channel. Elytra with surface moderately, densely and finely punctured and pubescent, punctures more coarse, dense, and asperate near scutellum; surface between punctures smooth and polished. Abdomen broad at base, slightly





Figs. 89-92. Male genitalia of North American Falagriini. 89. *Myrmecocephalus caviceps*. 90. *M. pinalicus*. 91. *Falagria dissecta*. 92. *F. sulcata*.

narrower than elytra. Terga III-V moderately strongly and transversely impressed at base; impressions coarsely foveate (Fig. 57); basins of foveae nearly smooth (or slightly granulose) and shining (Fig. 58). Tergal surfaces moderately densely punctured, punctures fewer and more asperate on basal segments; surface between punctures smooth and polished.

*Male.* Eighth tergite with apical margin broadly arcuate at middle, with comb of denticles. Eighth sternite with apical margin broadly and evenly rounded. Median lobe of aedeagus as in Figure 96A. Paramere as in Figure 96B.

*Female.* Eighth tergite and sternite with apical margins as in male. Spermatheca as in Figure 117.

*Type material.* *Falagria scutellaris* LeConte. Holotype, with labels as follows: pink disc [=Middle States]/Coney Isl., Aug./Type 6238/"*Falagria scutellaris*." The specimen is in the LeConte collection of the Museum of Comparative Zoology, Harvard University, Cambridge.

*Chitalia granulosa* Casey. Holotype, with labels: "Miss" [=Vicksburg, Miss.]/CASEY bequest 1925/Type USNM 38905/"*granulosa* Csy." The specimen is in the U.S. National Museum (Natural History), Washington.

*Chitalia illustris* Casey. Holotype, with labels as follows: "Miss" [=Vicksburg, Miss.]/CASEY bequest 1925/Type USNM 38906/"*illustris* Csy." The specimen is in the U.S. National Museum (Natural History), Washington.

*Distribution.* *Aleodorus scutellaris* is widely distributed in eastern North America, from New Hampshire west to Michigan and Illinois and south to Louisiana (Map 12). Specimens have been collected from March through October.

*Synonymy.* The holotypes of both *granulosa* and *illustris* are identical to that of *scutellaris* with respect to the narrow (or broad in some specimens), impressed median channel of the scutellum. On the basis of this character, they are synonymized.

*Material examined.* 62 specimens. CANADA: *Ontario*: Kent Co., Tilbury, May (FMNH) 1. UNITED STATES: *Illinois*: Pine Hills Field Sta., Union Co., May (CNCI) 22; Volo Bog, Lake Co., March (CNCI) 10. *Louisiana*: Concordia Co., 5 mi W Ferriday, May (CNCI) 3. *Maryland*: Baltimore, July (CASC) 2. *Massachusetts*: Marion, August, September (MCZC) 8. *Michigan*: Detroit, September (MSUC) 1; Rose Lake Wildlife Expt. Sta., Clinton Co. and Shiawassee Co., October (ERHC) 2. *New Hampshire*: Bretton Woods (CASC) 1. *Tennessee*: state label only (USNM, DFW) 12.

*Habitat.* There are no details known about the biology and habitat of this species.

*Remarks.* Since its original description (LeConte, 1866, p. 370), this species has been considered conspecific with *bilobatus*. The presence of several, closely spaced, heavily sclerotized ridges on the inner surface of the paramere of the male genitalia (Fig. 96B), and the broad, smooth, impressed median channel of the scutellum serve to distinguish *scutellaris* from *bilobatus*. Herein, I recognize *scutellaris* as a valid species.

*Aleodorus bilobatus* (Say)

Figs. 18, 29, 74, 97, 118; Map 4

*Aleochara bilobata* Say, 1830, p. 60 [original type locality, Missouri and Indiana; neotype locality, Indiana, Indianapolis]; 1839, p. 157.

*Aleodorus bilobatus*; Bland, 1865, p. 392; Fenyes, 1912, p. 20; 1918, p. 21; Jaques, 1951, p. 106.

*Chitalia bilobata*; Casey, 1906, p. 235; Blatchley, 1910, p. 346.

*Chitalia canadensis* Casey, 1906, p. 236 [type locality, Canada, Ottawa].

*Chitalia nigrescens* Casey, 1906, p. 236 [type locality, Iowa, Iowa City].

*Chitalia turbata* Casey, 1911, p. 176 [type locality, New Jersey, Elizabeth].

*Diagnosis.* Adults of *Aleodorus bilobatus* are extremely similar in appearance to those of the sympatric *scutellaris*, but may be readily distinguished from the latter by the uniformly and coarsely granulose scutellum, which is only slightly parted along the median line by a fine impressed line in some specimens.

*Description.* Length 2.8–4.1 mm ( $N = 85$ ;  $\bar{x} = 3.24$  mm). Color light to dark piceous-brown or piceous-black; head and tergal impressions darker; terga VI and VII also darker; mouthparts, basal antennal segments and legs generally paler. Habitus as in Figure 18.

Head (Fig. 18) little longer than wide, as wide as prothorax, sides slightly arcuate, parallel, arcuate-truncate at base, basal angles broadly rounded. Punctuation and pubescence fine and sparse on dorsum, occiput with more asperate punctures, narrow median area between and behind antennae devoid of punctures; surface between punctures smooth and shining. Eyes equal to length of temples. Antenna stout, moderately long, reaching middle of elytra or slightly beyond. Prothorax (Fig. 18) about as wide as head, broadest across anterior third, narrowing and converging strongly towards base, lateral margins strongly sinuate, posterior margin broadly emarginate. Disc strongly sulcate along median line except extreme apex, sulcus ending in subbasal fovea. Surface finely, sparsely punctured and pubescent, punctures tending to be more asperate and dense towards sulcus; surface between punctures smooth and shining. Scutellum flat, densely punctured, punctures asperate; punctures parted along median line by a fine, narrow line in some specimens. Elytra with surface minutely and moderately punctured and pubescent, punctures towards scutellum more dense and slightly asperate; surface between punctures smooth and polished. Abdomen broad at base, nearly as broad as elytra. Terga III–V very strongly and transversely impressed at base; impressions coarsely foveate; basins of foveae shining and smooth or slightly punctulate (appearing slightly granulate). Tergal surfaces moderately punctured, punctures asperate, more strongly so towards base; surface between punctures smooth and shining.

*Male.* Eighth tergite with apical margin broadly arcuate at middle, with comb of denticles (Fig. 74). Eighth sternite with apical margin broadly, evenly rounded. Median lobe of aedeagus as in Figure 97A. Paramere as in Figure 97B.

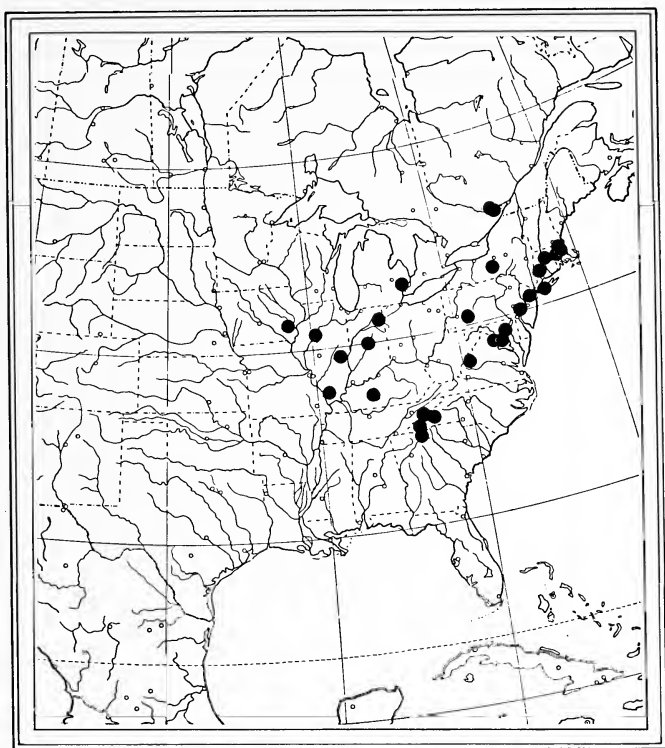
*Female.* Apical margin of eighth tergite and sternite as in the male. Spermatheca as in Figure 118.

*Type material.* *Aleochara bilobata* Say. Say's type of this species undoubtedly has been lost or destroyed. I have designated, as neotype of this species, a specimen in the Fall collection in the Museum of Comparative Zoology, Harvard University, with the labels: Ind./Indianapolis, 7/14-10/4117 det. A. Fenyès/H. C. Fall collection; my neotype designation label is attached to it.

*Chitalia canadensis* Casey. Lectotype, here designated, with labels as follows: "W.H.H., Ottawa, Can.,"/CASEY bequest 1925/Type USNM 38902/"canadensis Csy."; my lectotype designation label is attached to it. Two paralectotypes have the same label data as the lectotype.

*Chitalia nigrescens* Casey. Holotype, with the following labels: "Iowa City, Wickham"/CASEY bequest 1925/Type USNM 38903/"nigrescens Csy."

*Chitalia turbata* Casey. Holotype, with labels as follows: "Elizabeth, N.J.,"/CASEY bequest 1925/Type USNM 38904/"turbata Csy."



Map 14. Distribution of *A. bilobatus*.

Type specimens of the above three species are in the Casey collection in the U.S. National Museum (Natural History), Washington.

*Distribution.* *Aleodorus bilobatus* occurs throughout eastern North America, from Ontario and southern New England south to North Carolina and Georgia and west to Illinois and Iowa (Map 14). Specimens have been collected from March to November.

*Material examined.* 277 specimens. CANADA: *Ontario*: Merivale, April (CNCI) 6; Ottawa (CNCI) 5; Hull (CNCI) 1; country label only (USNM) 3. UNITED STATES: *Connecticut*: Cornwall, April (CNCI, CUIC) 8. *District of Columbia*: Washington (MCZC, USNM) 5; Washington, November (USNM) 2; Mt. Hamilton, November (USNM) 1; Washington (INHS) 1; Rosslyn, Washington, March (USNM) 1. *Georgia*: Clayton, 2,000–3,700 ft, June (AMNH) 2. *Illinois*: Pine Hills Field Sta., Union Co., May (CNCI) 1; Charleston, October (INHS) 3; Peoria, October (INHS) 1; state label only (INHS, DEFW, AMNH) 14. *Indiana*: Indianapolis, July (MCZC) 1; Mineral Springs, September (USNM) 1; Marion Co., April (CASC) 1; Fort Wayne, Allen Co., August (UCRC) 2. *Iowa*: Iowa City, October (FMNH) 1. *Kentucky*: Mammoth Cave Nat'l. Park, Edmonton Co., March (FMNH) 5. *Maryland*: Bladensburg, September



(USNM) 1; Freshet, Plummer's Isl., March (USNM) 2; College Park, April (USNM) 1; Plummer's Isl., April, September, October (USNM) 4; Sparrow Point, September (CASC) 1; Baltimore, July (CASC) 1; Annapolis, January (USNM); Prince Georges Co., Beltsville, May (JHFC) 1; Prince Georges Co., Patuxent Wildlife Refuge, June (DENH) 10; state label only (DEFW) 4. *Massachusetts*: Springfield, April, September (USNM, MCZC) 2; Swansea (MCZC) 1; Lowell (MCZC) 4; Beverly (MCZC) 1; Tyngsboro, April, December (MCZC, MSUC) 3; Framingham, November (CASC, MCZC, USNM) 6; Sherborn, May (MCZC) 1; Arlington, May (MCZC) 2; state label only (INHS, MCZC) 7. *Michigan*: Detroit, October (USNM, SEMC, MCZC) 17; Clarkston, October (USNM) 1; state label only (MCZC) 6. *Pennsylvania*: Darby, March (CASC) 11; Belfast, May (CASC) 1; Manyuak, March (CASC) 1; Jeannette, July (ICCM) 1. *New Jersey*: Union, April, November (AMNH) 5; Roselle, April (AMNH, USNM) 10; Elizabeth, November (MCZC) 1; Snake Hill (AMNH) 8; Angelsea, March (MCZC) 2; Monmouth, October (USNM) 2; Roselle Park, March, April (AMNH, USNM) 2; Hackensack (CASC) 1; Berkeley Heights, May (AMNH) 1; Tenaflly (CUIC) 1; state label only (AMNH) 1. *New York*: Rockaway Beach, Long Island (NYSM) 5; Mendon, May (CUIC) 2; Zurich, Wayne Co., October (AMNH) 1; Mosholu (AMNH) 1; McLean Bog, April (ERHC) 1; Howlett, L.I., May (USNM) 3; Wyandanch, L.I., November (USNM, CUIC) 2. *North Carolina*: Mt. Pisgah, October (NYSM) 6; Black Mts., September, October (AMNH) 31; Highlands, June (MCZC) 1; Retreat, June (USNM) 1. *Tennessee*: Cocke Co., 6 mi SE Cosby, May (DENH) 1. *Virginia*: Warm Springs (AMNH) 3; Chain Bridge, September (USNM) 1; Glencarlyn, September (MCZC) 1; Alex Co., September (MCZC) 1; Fredricksburg, April (USNM) 1; Falls Church, October, November (USNM) 18; state label only (DEFW) 2. *West Virginia*: Ft. Pendleton, July (USNM) 1.

*Habitat*. The species is known to occur in wet biotopes. Blatchley (1910, p. 346) claimed that specimens have been taken beneath bark and by sifting vegetable debris in moist woods. Specimens at hand have been taken from along a riverbank and in a swamp, from dead grass, from leaf litter piled in a fence row and in a ditch of a mesic forest, from moss, and in a duff sample.

#### 8. *Lissagria* Casey

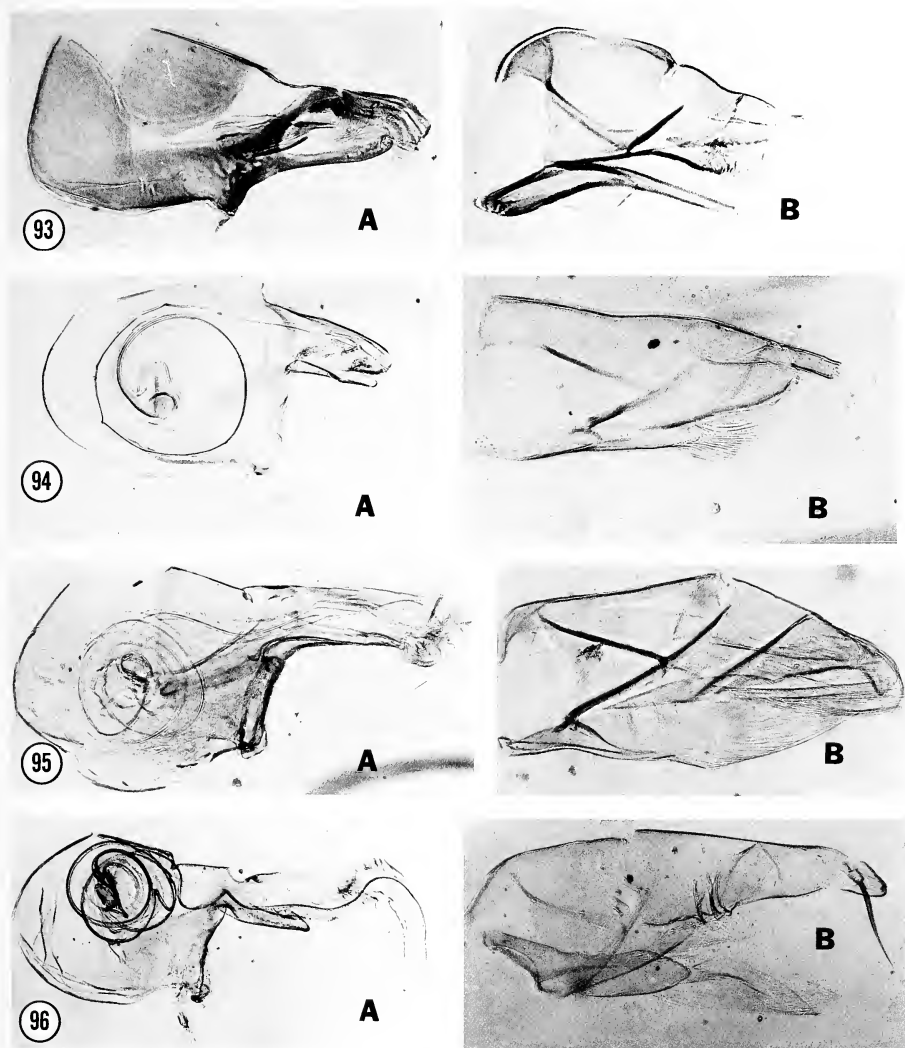
*Lissagria* Casey, 1906, p. 252 (proposed as subgenus of *Falagria*); Seevers, 1978, p. 145.

As subgenus of *Falagria*: Fenyess, 1912, pp. 21, 23, 26; 1920, p. 155; Leng, 1920, p. 124; Notman, 1920, p. 731; Bernhauer and Scheerpeltz, 1926, p. 579; Bradley, 1930, p. 313; Scheerpeltz, 1934, pp. 1572, 1574; Blackwelder, 1952, p. 223; Arnett, 1968, p. 289; Moore and Legner, 1975, p. 414.

*Type-species*: *Falagria laeviuscula* LeConte, fixed by subsequent designation (Fenyess, 1912, p. 23).

*Omoschema* Notman, 1920, p. 731; Bernhauer and Scheerpeltz, 1926, p. 579; Blackwelder, 1952, p. 274; Arnett, 1968, p. 289; Moore and Legner, 1975, p. 461; Seevers, 1978, p. 148. **New Synonym.**

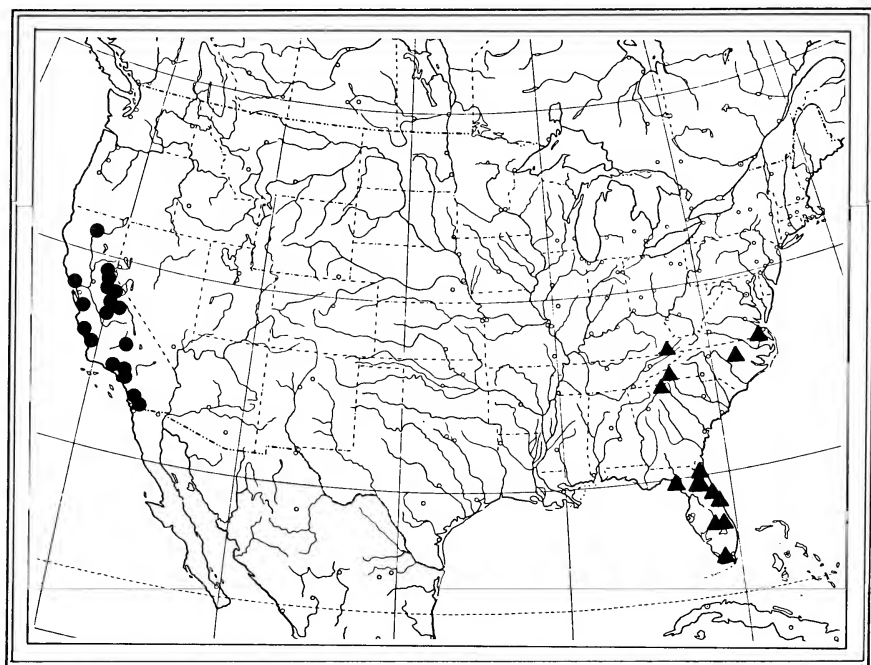
*Type-species*: *Omoschema laticeps* Notman, fixed by monotypy (Notman, 1920, p. 731).



Figs. 93–96. Male genitalia of North American Falagriini. 93. *Leptagria perexilis*. 94. *Aleodorus partitus*. 95. *A. intricatus*. 96. *A. scutellaris*.

**Diagnosis.** Adults of *Lissagria* may be easily distinguished from those of other Falagriini by the dense punctation of the elytra adjacent to the scutellum, presence of an arcuate row of denticles on the apical margin of tergum VIII, hypomera not delimited by a marginal ridge, and the simple, unmodified scutellum.

**Description.** Head moderately small, rounded or arcuate-truncate behind, slightly flattened dorsally or convex. Neck very slender, scarcely more than  $\frac{1}{4}$  as wide as



Map 15. Distribution of *Lissagria laeviuscula* (circles) and *L. laticeps* (triangles).

head across eyes. Eyes rather small, but slightly prominent. Labrum (Fig. 30A) transverse, angles broadly rounded, anterior margin truncate. Mandibles (Fig. 30D, E) robust, stout, apex curved; right mandible with small, obscure tooth at middle of inner margin; left mandible simple. Maxilla (Fig. 30C) with galea longer than lacinia, densely pubescent on membranous apex; lacinia with several elongate spines at apex, densely pubescent below spines. Maxillary palpus (Fig. 30C) slender; segment 3 longer than 2, broadened apically; segment 4 elongate, subuliform. Mentum transverse, broadly emarginate along anterior margin. Ligula (Fig. 30B) bifid; lobes rounded apically. Labial palpus (Fig. 30B) elongate; segment 1 long, broader than other segments; segment 2 short; segment 3 longer than 2, filiform. Antenna moderately long, gradually and slightly broadened distally; segments 2 and 3 elongate, subequal in length; segments 5–10 gradually transverse; segment 11 not quite as long as 9 and 10 combined. Prothorax slightly to moderately narrowed at base, evenly convex to somewhat flattened. Disc finely to deeply sulcate along median line except at apex, sulcus ending basally in a large, deep, round to transverse fovea. Prosternum moderately large in front of procoxae, posterior margin broadly angulate at middle. Mesospiracular peritremes (Fig. 80) moderately large, inner margins broadly rounded in most specimens, nearly attaining median line. Mesosternal process extending to middle of mesocoxae, broadly to acutely rounded at apex, slightly separated from metasternal projection by a short, scarcely depressed isthmus or isthmus absent.

Mesocoxae moderately separated. Hypomera not delimited from pronotal disc by a marginal ridge. Scutellum simple, flat, and densely punctured and pubescent, without carinae or medial impunctate groove. Elytra longer and broader than prothorax, convex, densely punctate near scutellum. Abdomen rather broad at base, not quite as broad at base as elytra. Terga III–V broadly impressed at base; impressions impunctate or with a few obsolete punctures. Apical margin of tergum VIII with an arcuate row of small denticles.

At present, the genus *Lissagria* is known only from North America, with two species occurring north of Mexico.

*Synonymy.* *Omoschema* is here considered a junior synonym of *Lissagria*. The characters given by Notman (1920) as diagnostic for *Omoschema* are basically the same as those for *Lissagria*. Seevers (1978) separated the two genera in his key on the basis of differences in the relative length of the mesosternal process, shape of the pronotum, and head shape. I regard these differences as extremely slight and insufficient to separate genera.

#### KEY TO SPECIES OF *Lissagria*

1. Small, most specimens less than 3.0 mm; pronotal sulcus deep, ending in a deep, round fovea; head arcuate-truncate at base; known from southern United States ..... *laticeps* (Notman)
- Larger, most specimens greater than 3.0 mm; pronotal sulcus fine and shallow, ending in a large, transverse shallow fovea; head broadly rounded at base; known from California ..... *laeviuscula* (LeConte)

#### *Lissagria laticeps* (Notman), **New Combination**

Figs. 19, 38, 62, 99, 120; Map 15

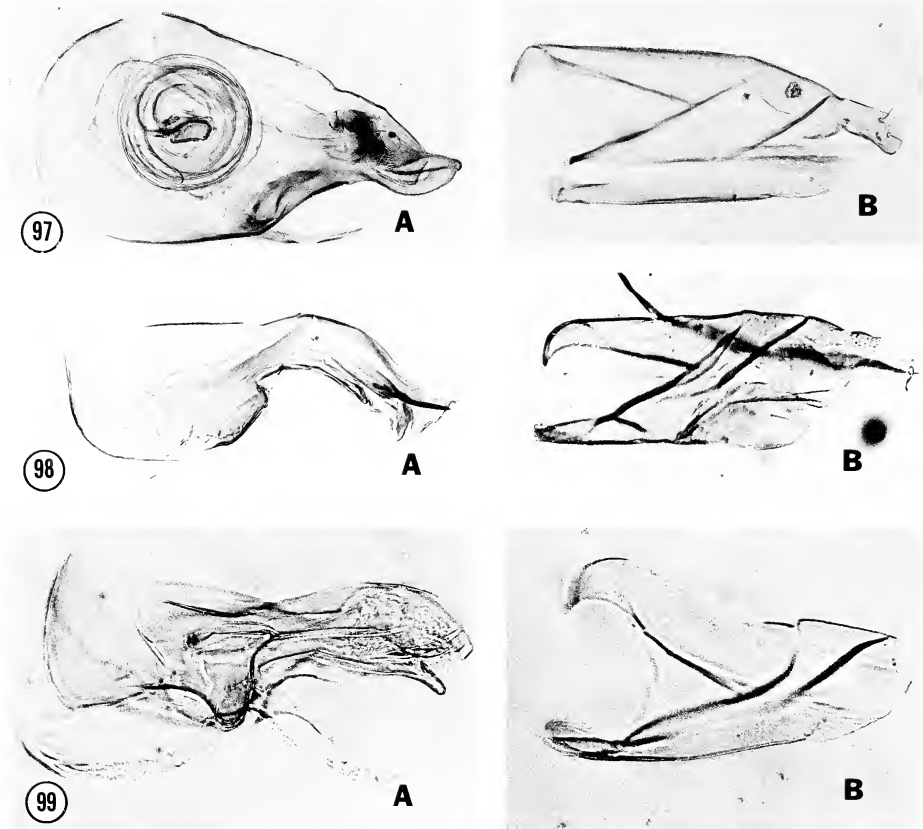
*Omoschema laticeps* Notman, 1920, p. 732 [type locality, Florida, Titusville]; Bernhauer and Scheerpeltz, 1926, p. 579; Arnett, 1968, p. 289; Seevers, 1978, p. 277.

*Diagnosis.* *Lissagria laticeps* is readily separated from *laeviuscula* by its allopatric southern distribution, smaller body size (<3.0 mm), deep pronotal sulcus terminating in a deep round fovea, and distinctive dorsal habitus (Fig. 19).

*Description.* Length 1.80–2.80 mm (N = 19;  $\bar{x}$  = 2.30 mm). Color light to dark ferruginous; 1 or 2 basal antennal segments, apical antennal segment (whitish in most specimens), legs and mouthparts paler. Habitus as in Figure 19.

Head small, arcuate-truncate at base, hind angles obtusely rounded, sides subparallel. Surface moderately densely punctured; pubescence moderately dense and fine; surface between punctures smooth and shining. Eyes equal to length of temples. Antenna reaching to apex of elytra. Prothorax (Fig. 38) slightly longer than head, broadest anteriorly, narrowing and converging posteriorly; anterior angles broadly and evenly rounded; lateral margins broadly sinuate along posterior half; posterior margin evenly arcuate, very finely reflexed. Disc moderately sulcate along median line except at apex, sulcus ending in a deep, round fovea. Surface finely but densely punctured and pubescent; surface between punctures smooth and shining. Scutellum (Fig. 38) flat, simple, and densely punctured and pubescent. Elytra with surface finely and uniformly punctured and pubescent except for dense punctation near scutellum.





Figs. 97-99. Male genitalia of North American Falagriini. 97. *Aleodorus bilobatus*. 98. *Lissagria laeviuscula*. 99. *L. laticeps*.

Abdomen (Fig. 62) broad at base, slightly narrower than elytra. Terga III-V shallowly impressed at base; impression of tergum III with many obsolete punctures (Fig. 62); impressions of terga IV and V impunctate. Tergal surfaces densely and finely punctured and pubescent; surface between punctures smooth and polished.

*Male*. Eighth tergite with apical margin broadly arcuate at middle with comb of denticles. Eighth sternite with apical margin broadly and evenly rounded. Median lobe of aedeagus as in Figure 99A. Paramere as in Figure 99B.

*Female*. Eighth tergite and sternite with apical margin as in male. Spermatheca as in Figure 120.

*Type material*. Holotype, with labels as follows: "Titusville, Fla., Nov 8-11"/TYPE/"*Omoschema laticeps*, n.g. n.sp." The specimen is in the collection of the American Museum of Natural History, New York.

*Distribution*. *Lissagria laticeps* occurs throughout southeastern United States and

is common along coastal areas from Virginia south to Florida (Map 15). Specimens have been collected from March through July.

*Material examined.* 37 specimens. UNITED STATES: *Florida*: Enterprise, May–June (USNM, MCZC) 13; Sand Point (USNM) 1; Highlands Co., SW shore of Lake Istokpoga, June (FMNH) 2; Dade Co., Everglades Nat'l. Park, Mahogany Hammock, June (FMNH) 2; Jacksonville, March (AMNH, FMNH) 4; Lake Istokpoga, N. L. Placid, March (CNCI) 5; Okeechobee, July (FMNH) 2; Taylor Co., 11 mi NW Steinhatchee, May (DENH) 3; Putnam Co., Welaka Exp. Sta., May (DENH) 1. *Georgia*: Clayton, 2,000–3,000 ft, June (FMNH) 1. *North Carolina*: Wake Co., Reedy Cr. S.P., May (NCSU) 1; Valley of Black Mts., July, August (AMNH) 4. *Virginia*: Jones Cr., Lee Co. (USNM) 1; Lake Drummond, June (USNM) 2.

*Habitat.* Specimens at hand have been taken by sifting lakeshore debris, and from berlese samples of forest floor litter and debris under pine bark.

*Lissagria laeviuscula* (LeConte)

Figs. 20, 30, 42, 49, 61, 75, 80, 98, 119; Map 15

*Falagria laeviuscula* LeConte, 1866, p. 371 [type locality, California, Fort Tejon].

*Lissagria laeviuscula*; Casey, 1906, p. 252; Fenyess, 1920, p. 155; Notman, 1920, p. 731; Bernhauer and Scheerpeltz, 1926, p. 579; Scheerpeltz, 1934, p. 1574; Moore and Legner, 1975, p. 414; Seevers, 1978, p. 145.

*Lissagria fissilis* Casey, 1906, p. 254 [type locality, California, Giant Forest, Tulare Co.].

*Lissagria impressifrons* Casey, 1906, p. 254 [type locality, California, Sta. Cruz Mts.].

*Lissagria robusta* Casey, 1906, p. 254 [type locality, California, Sta. Cruz Mts.].

*Lissagria minuscula* Casey, 1906, p. 254 [type locality, California, Los Angeles Co.].

*Lissagria longicollis* Casey, 1906, p. 255 [type locality, California, Lake Co.].

*Diagnosis.* This species may be distinguished from *laticeps* by the allopatric western distribution, larger adult size (most specimens greater than 3.0 mm), shallow pronotal sulcus terminating in a transverse fovea, and characteristic male and female genitalia (Figs. 98 and 119).

*Description.* Length 2.7–3.6 mm (N = 100;  $\bar{x}$  = 3.03 mm). Color rufo-ferrugineous to dark rufo-piceous; terga VI–VIII darker; antennae, legs and mouthparts paler. Habitus as in Figure 20.

Head (Fig. 20) relatively small, broadly rounded at base, hind angles broadly rounded. Surface minutely and sparsely punctured and pubescent; surface between punctures smooth and shining. Eyes prominent, shorter than length of temples. Antenna long, nearly reaching apex of elytra. Prothorax (Fig. 20) elongate, very slightly longer than head, scarcely narrowed and converging towards base; anterior angles evenly rounded; lateral margins nearly straight or slightly sinuate; posterior margin evenly truncate. Disc distinctly sulcate along median line except extreme apex, sulcus ending in a broad, transverse impression or fovea. Surface sparsely and finely punctured and pubescent; surface between punctures smooth and polished. Scutellum large, flat, and unmodified; surface with dense asperate punctures, moderately pubescent. Elytra with surface finely and evenly punctured and pubescent, except area of extremely dense punctation adjacent to scutellum (Fig. 49); surface

between punctures smooth and shining. Abdomen (Fig. 61) broad at base, nearly as wide as elytra. Terga III–V transversely impressed at base; impressions of terga III and IV with distinct, separated, coarse, but shallow punctures; impression of tergite V impunctate. Tergal surfaces with fine, asperate punctures, and finely pubescent; surface between punctures smooth and polished.

*Male.* Eighth tergite with apical margin broadly arcuate at middle with comb of denticles (Fig. 75). Eighth sternite with apical margin broadly rounded. Median lobe of aedeagus as in Figure 98A. Paramere as in Figure 98B.

*Female.* Eighth tergite and sternite with apical margin as in male. Spermatheca as in Figure 119.

*Type material.* *Falagria laeviuscula* LeConte. Holotype, with labels as follows: "Cal."/Type 6240/"F. laeviuscula LeC." The specimen is in the Leconte collection of the Museum of Comparative Zoology, Harvard University, Cambridge.

*Lissagria fissilis* Casey. Holotype, with the following labels: "Giant Forest, Tulare Co., Cal.,"/CASEY bequest 1925/TYPE USNM 38929/"fissilis Csy."

*Lissagria robusta* Casey. Lectotype, here designated, with the labels: "Sta. Cruz Mts., Cal.,"/CASEY bequest 1925/TYPE USNM 38930/"robusta Csy."; my lectotype designation label is attached to it. Two paralectotypes have the same label data as the lectotype. In addition, one paralectotype has the labels: "Cal." [=Monterey, Monterey Co.], while two others are labeled "Cal."

*Lissagria minuscula* Casey. Lectotype, here designated, with labels as follows: "Los Angeles Co., Cal.,"/CASEY bequest 1925/Type USNM 38932/"minuscula Csy."; my lectotype designation label is attached to it. One other paralectotype has identical labels to the lectotype.

*Lissagria longicollis* Casey. Holotype, with the labels: "Lake Co., Cal.,"/CASEY bequest 1925/TYPE USNM 38933/"longicollis Csy."

*Lissagria impressifrons*. Holotype, with the following labels: "Sta. Cruz Mts., Cal.,"/CASEY bequest 1925/TYPE USNM 38931/"impressifrons Csy.,"/CASEY determ., robusta-7.

Type specimens for the above five species are in the Casey collection of the U.S. National Museum (Natural History), Washington.

*Distribution.* *Lissagria laeviuscula* occurs throughout California, especially at high elevations (Map 15). Specimens have been collected from January through December; however, most specimens have been taken in June, July, and August.

*Material examined.* 678 specimens. UNITED STATES: *California*: Los Angeles Co., San Gabriel Mts., San Dimas Cyn., June, July (INHS) 113; Los Angeles Co., San Gabriel Mts., San Dimas Cyn., August, 1,200 ft. (INHS) 90; 12 mi N of Escondido, San Diego Co., September (INHS) 9; Rancho Santa Ana Bot. Garden, Claremont, September (INHS) 3; Evey Canyon, 4 mi NNE of Claremont, May (INHS) 2; Evey Cyn., Los Angeles Co., September (INHS) 3; Santa Ana Mts., Riverside Co., May, 2,000 ft (INHS) 16; Santa Ana Mts., W of Elsinor, Riverside Co., June (INHS) 15; Yosemite Nat'l. Park, August (INHS) 2; Pasadena, January, March, September, October, December (MCZC, CASC, LACM, FMNH) 31; Pasadena (AMNH) 2; Pomona Mts., May, September (MCZC, AMNH) 7; Pomona, June (MCZC, FMNH) 2; Ojai, March (MCZC) 1; Amador Co., Tiger Creek, ENE of Pioneer, 3,500 ft, June (MCZC) 33; Amador Co., 1 mi W of Pine Grove, June (MCZC) 11; Amador Co., 1.3 mi W Pine Grove, 2,200 ft, May (MCZC) 2; Amador Co., Panther Ridge, 6,200

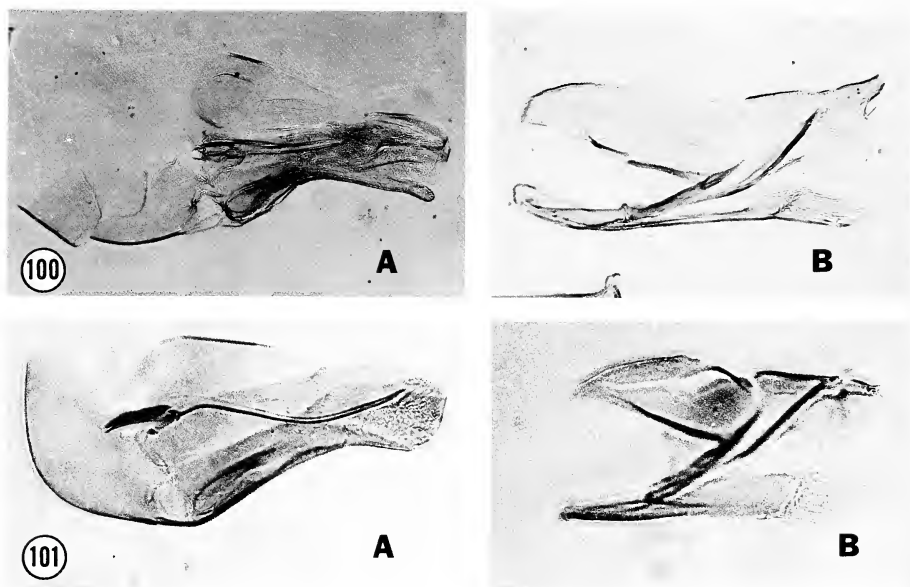
ft, June (MCZC) 1; "S. Cal." (MCZC, AMNH, SEMC) 7; Marion Co., August (USNM) 1; Shasta Co., October (USNM) 1; Sta. Cruz Mts. (USNM, CASC, CNCI) 24; San Mateo, August (USNM) 1; Mt. Wilson, June (USNM) 1; Los Gatos (USNM) 2; Calaveras Co., Big Trees, Alt. 5,000 ft, May, July (CASC) 40; Mokel. Hill, July (CASC) 1; Cuyamaca, San Diego Co., July (CASC) 2; Mt. Wilson, 2,000 ft, May (CASC, CNCI) 7; Mt. back of Alma, September, October (CASC, CNCI) 4; Murphys, Calaveras Co., 2,500 ft, May (CASC, CNCI) 5; Julian, San Diego Co., December (CASC) 1; Calaveras Co., 3 mi NE of Glencoe, 2,000 ft, June (MCZC) 1; Huntington Lake, Fresno Co., 7,000 ft, July (CASC) 2; Fresno Co., Sierra N.F., 4.4 mi SW Big Creek, 5,400 ft, May (MCZC) 1; San Diego Co., Torrey Pines, April (CASC) 1; Calaveras Co., 3 mi NW West Point, 2,250 ft, May (MCZC) 1; Licking Fork, Moke-lumne River, Calaveras Co., 2,900–3,100 ft, June (CASC) 3; Calaveras Co., Lampsons R., R.R. Flat, 1,800 ft, June (CASC) 1; Huntington Lake, Fresno Co., August (MCZC, CNCI) 11; San Diego Co., Santa Isabell, February (CNCI) 2; San Diego Co., Pine Valley, June (CNCI) 11; San Diego, Co., San Vicente Valley, June (CNCI) 1; San Diego Co., Lake Wohlford, April (CNCI) 1; Calaveras Co., Wool Hollow Cave, July (CNCI) 1; Eldorado Co., 5 mi SW of Kyburz, 4,000 ft, May (CNCI) 12; Poly Canyon, San Luis Obispo Co., October (CNCI) 68; Samuel P. Taylor St. Pk., May (CNCI) 1; San Luis Obispo Co., 8 mi E of Morro Bay, June (CNCI) 1; Mariposa Big Trees, May (CUIC) 2; Giant Forest, Sequoia Nat'l. Pk., July (CUIC) 1; Riverton, 3,000 ft, July, August (AMNH) 17; Sugar Pine (AMNH, FMNH) 4; Kern Co., 1 mi W of Glenville, Poso Creek, July (AMNH) 2; Shasta Co., Shingletown, September (AMNH) 1; Mariposa Co., Back Meadows, July (AMNH) 1; San Luis Obispo Co., San Simeon, July (AMNH) 2; Tuolumne Co., Strawberry, June, July (UCBC) 8; Mariposa Co., 2 mi S of Miami Ranger Sta., 4,000 ft, July (UCBC) 2; Tulare Co., Wood Lake, December (UCBC) 1; Tuolumne Co., Cow Creek, 5 mi NE of Strawberry, July (UCBC) 3; Mariposa Co., Wawona, July, 7,000 ft (UCBC) 1; Placer Co., 2 mi W of Colfax, October (UCRC) 1; Alpine, May (UCRC) 2; Monterey Co., Redwood Gulch, August (UCRC) 1; San Luis Obispo Co., Poly Canyon, October (UCRC) 2; Sequoia Nat'l. Pk., May, August (SEMC, LACM) 3; San Bernadino Mts., Cold Creek Ranch, July (LACM) 1; L.A. River, L.A., July (LACM) 1; Modesto, February (FMNH) 1; Miami, May (FMNH) 1; Los Gatos (FMNH) 1; Butte Co., 2 mi SW Stirling City, 2,900 ft, May (DENH) 19; Butte Co., Mountain House, May (DENH) 21; Butte Co., Jonesville, 5,300 ft, May (DENH) 5; Tulare Co., Sequoia N.P., 1.8 mi and 9.2 mi S Kaweah Camp, 5,800 and 3,200 ft, May (MCZC) 5; Napa Co., 10.1 mi N Calistoga, 1,900 ft, May (MCZC) 12; state label only, June (LACM) 1; state label only (FMNH) 2.

*Habitat.* This species appears to prefer wet habitats. Specimens at hand have been collected from flood debris along streams, from the base of cattails, from leaf mold near a swampy area, from various leaf litter in a mixed hardwood-conifer forest and along a stream, from dry moss of a conifer log, from oak duff, and with ants.

#### 9. *Borboropora* Kraatz

*Borboropora* Kraatz, 1862, p. 406; Mulsant and Rey, 1875, pp. 429, 431; Redtenbacher, 1874, p. 129; Gemminger and Harold, 1868, p. 502; Fowler, 1888, p. 147; Ganglbauer, 1895, p. 252; Everts, 1898, p. 230; Reitter, 1909, pp. 40, 74; Fenyes,





Figs. 100–101. Male genitalia of North American Falagriini. 100. *Borboropora quadriceps*. 101. *B. sulcifrons*.

1912, pp. 20, 21, 25; 1918, p. 18; 1920, p. 146; Leng, 1920, p. 124; Notman, 1920, p. 731; Porta, 1926, p. 151; Bernhauer and Scheerpeltz, 1926, p. 573; Scheerpeltz, 1929, p. 9; Portevin, 1929, pp. 253, 293; Scheerpeltz, 1930, p. 73; Bradley, 1930, pp. 85, 313; Joy, 1932, pp. 16, 39, 41; Scheerpeltz, 1934, p. 1569; Tottenham, 1949, p. 387; Blackwelder, 1952, p. 83; Horion, 1951, p. 168; Horion, 1967, p. 199; Arnett, 1968, p. 289; Palm, 1968, p. 76; Lohse, 1974, pp. 64, 67; Moore and Legner, 1975, p. 385; SeEVERS, 1978, p. 146.

Variant spellings: *Borboropora* Brisout, 1871, p. 140; *Borboropora* Fowler, 1888, p. 436; *Borboropora* Mulsant and Rey, 1876, p. 10.

Type-species: *Borboropora kraatzi* Fuss, fixed by monotypy (Kraatz, 1862, p. 406).

*Pseudoscopaeus* Weise, 1877, p. 8; FenyEs, 1912, p. 21; Blackwelder, 1952, p. 330.

Type-species: *Pseudoscopaeus reitteri* Weise, fixed by monotypy (Weise, 1877, p. 8).

*Aneurola* Casey, 1893, p. 347; 1906, p. 251; FenyEs, 1912, p. 21; Blackwelder, 1952; p. 52.

Type-species: *Aneurola sulcifrons* Casey, fixed by monotypy (Casey, 1893, p. 347).

*Orthagria* Casey, 1906, p. 260; FenyEs, 1912, p. 21; Blackwelder, 1952, p. 278.

Type-species: *Falagria quadriceps* LeConte, fixed by monotypy (Casey, 1906, p. 260).

Biology: Chabanaud, 1905, pp. 206–207 (*kraatzi*).

*Diagnosis.* Adults of the genus *Borboropora* are distinguished from those of other Falagriini by the large, subquadrate head (Figs. 21–22), which is longitudinally impressed at the vertex and with a longitudinal fovea or impression on the front between the eyes in many specimens, apical margin of the eighth tergite with an arcuate comb of denticles, unlimited hypomera, and area of dense punctation near the scutellum (Fig. 50).

*Description.* Head large, subquadrate, truncate at base, angles narrowly rounded; median line deeply impressed anterior to middle in most specimens. Neck very slender, scarcely  $\frac{1}{4}$  as wide as head across eyes. Eyes rather small. Labrum (Fig. 31A) strongly transverse, angles rounded. Mandibles (Fig. 31D, E) slender, prominent, curved at apex; right mandible with 2 strong, uneven teeth at middle of inner margin; left mandible with 1 tooth at middle of inner margin. Maxilla (Fig. 31C) with galea about as long as lacinia, densely ciliate on membranous apex; lacinia with a few elongate and curved spines below apex, densely ciliate below spines. Maxillary palpus (Fig. 31C) very slender; segment 3 longer, but scarcely wider than 2; segment 4 rather long, subuliform. Mentum transverse, subtruncate in front. Ligula (Fig. 31B) bifid. Labial palpus (Fig. 31B) elongate; segment 1 very long, wider than other segments; segment 2 very short, narrower than 1; segment 3 much longer than 2. Antenna moderate in length, more or less incrassate towards apex; segments 1–3 gradually decreasing in length; penultimate segments more or less transverse; segment 11 not as long as 9 and 10 combined. Prothorax large, subquadrate, moderately narrowed at base. Disc feebly convex, finely and feebly impressed and sulcate along median line. Prosternum moderately large before procoxae, posterior margin broadly angulate. Mesospiracular peritremes large, quadrate, contiguous along median line. Mesosternal process rather broad, arcuate-truncate at apex, not quite attaining middle of mesocoxae. Metasternal process transversely convex, sinuate at apex, rather long, separated from mesosternal process by a short isthmus in most specimens. Mesocoxae rather broadly to narrowly separated. Hypomera not delimited from disc by marginal ridge. Scutellum flat, unmodified, coarsely granulose. Elytra longer and broader than prothorax, parallel-sided; area of dense, coarse punctation adjacent to scutellum. Abdomen elongate, somewhat dilated behind. Terga III–V transversely impressed at base; impressions impunctate, smooth. Apical margin of tergum VIII with arcuate comb of minute denticles.

Known species of the genus *Borboropora* are distributed in the Holarctic region. Two species occur in America north of Mexico.

#### KEY TO SPECIES OF *Borboropora*

1. Large, length greater than 2.2 mm; widely distributed in eastern North America . . . .  
     ..... *quadriceps* (LeConte)
- Extremely small, length under 1.4 mm; known from Florida ..... *sulcifrons* (Casey)

#### *Borboropora quadriceps* (LeConte)

Figs. 21, 31, 39, 46, 50, 63, 100, 120; Map 16

*Falagria quadriceps* LeConte, 1866, p. 371 [type locality, New York].

*Orthagria quadriceps*; Casey, 1906, p. 260.

*Borboropora quadriceps*; Fenyès, 1912, p. 25; 1920, p. 147; Leng, 1920, p. 124; Bernhauer and Scheerpeltz, 1926, p. 573; Moore and Legner, 1975, p. 385; SeEVERS, 1978, p. 277.

*Borboropora grandis* Bernhauer, 1905, p. 21 [type locality, America borealis].

*Diagnosis.* This species is easily separated from *sulcifrons* by the greater body size, distinctive habitus (Fig. 21), and allopatric eastern distribution (Map 16).

*Description.* Length 2.25–3.3 mm ( $N = 36$ ;  $\bar{x} = 2.77$  mm). Body elongate, depressed; color rufo-brunneous to piceous-black; mouthparts, basal 2 or 3 antennal segments, humeral angles, apical third of elytra and legs paler in most specimens. Habitus as in Figure 21.

Head very large, subquadrate, sides parallel, straight, wider than prothorax, only slightly longer than wide, arcuate-truncate at base, basal angles acutely rounded. Surface sparsely to coarsely punctured and pubescent; frons along median line behind antennal insertions with shallow, longitudinal fovea or impression; base of vertex along median line usually distinctly impressed and sometimes excised. Eyes slightly prominent, shorter than length of temples. Antenna moderate in length, reaching basal  $\frac{1}{3}$  of elytra. Prothorax (Fig. 39) large, subquadrate, moderately narrowed behind, slightly narrower than head; anterior angles broadly, evenly rounded; lateral margins slightly sinuate posteriorly; posterior angles sometimes produced into a minute projection; posterior margin nearly straight or slightly arcuate at middle, finely margined. Disc moderately to strongly sulcate along median line except extreme apex, sulcus ending in a shallow, broad and somewhat transverse fovea. Surface finely and sparsely punctured and pubescent; surface between punctures polished and shining. Scutellum (Figs. 39, 46) broadly flattened or slightly convex, coarsely and densely punctured. Elytra with surface finely, moderately punctured and pubescent, except area of dense, coarse punctation near scutellum (Fig. 50). Abdomen broad at base, slightly narrower than elytra. Terga III–V broadly, transversely impressed at base; basal impressions smooth, shining and impunctate (Fig. 63). Tergal surfaces at apex moderately and coarsely punctured and pubescent; surfaces at base finely and sparsely punctured; surface between punctures smooth and shining.

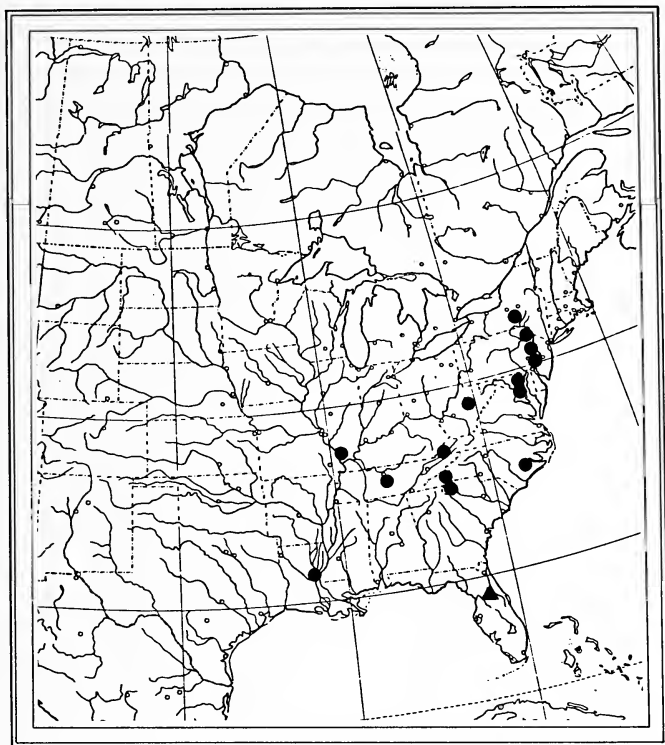
*Male.* Eighth tergite with apical margin broadly arcuate at middle with comb of denticles. Apical margin of eighth sternite broadly, evenly rounded. Median lobe of aedeagus as in Figure 100A. Paramere as in Figure 100B.

*Female.* Eighth tergite and sternite with apical margin as in the male. Spermatheca as in Figure 121.

*Type material.* *Falagria quadriceps* LeConte. Holotype, with labels as follows: "N.Y., Apl."/Type 6241/"F. quadriceps LeC." The specimen is in the LeConte collection of the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

*Borboropora grandis* Bernhauer. Lectotype, here designated, with labels as follows: "Nordamerika, leg. Pöpp. 1853"/Coll. Mus. Vind. ded. Ganglb./"grandis Bernh. Typus"/Chicago NHMus, M. Bernhauer Collection; my lectotype designation label is attached to it. The specimen is in the Field Museum of Natural History, Chicago.

*Distribution.* *Borboropora quadriceps* occurs in eastern North America, from New York south to North and South Carolina and west to Illinois and Louisiana (Map 16). Specimens have been collected from April to July, and September to October, but with most collections in July.



Map 16. Distribution of *Borboropora quadriceps* (circles) and *B. sulcifrons* (triangles).

*Material examined.* 36 specimens. UNITED STATES: *District of Columbia*: Washington, April, July (USNM) 2; D.C. (MCZC, FMNH) 2. *Illinois*: Pine Hills Field Sta., Union Co., May (CNCI) 4; Union Co., Pine Hills, nr. McCann Sprgs., May (CNCI) 2. *Louisiana*: Concordia Co., 5 mi W of Ferriday, May (CNCI) 1. *Maryland*: Jackson's Isl., June (USNM) 1; Oakland, July (USNM) 1; Deer Park, July (USNM, FMNH) 2. *North Carolina*: Maysville, October (CUIC) 1; Black Mt., September (AMNH) 1. *Pennsylvania*: Chestnut Hill, July (MCZC) 2; Wind Gap, July (CASC) 1; Camp Colang, Pike Co., July (FMNH) 1. *South Carolina*: Clemson, April (CNCI) 3. *Tennessee*: State label only (DEFW) 1. *Virginia*: Stone Cr., Lee Co. (USNM) 1; Straight Cr., Lee Co. (USNM) 1; state label only (USNM, MCZC) 5. *West Virginia*: Fort Pendleton, July (USNM) 1.

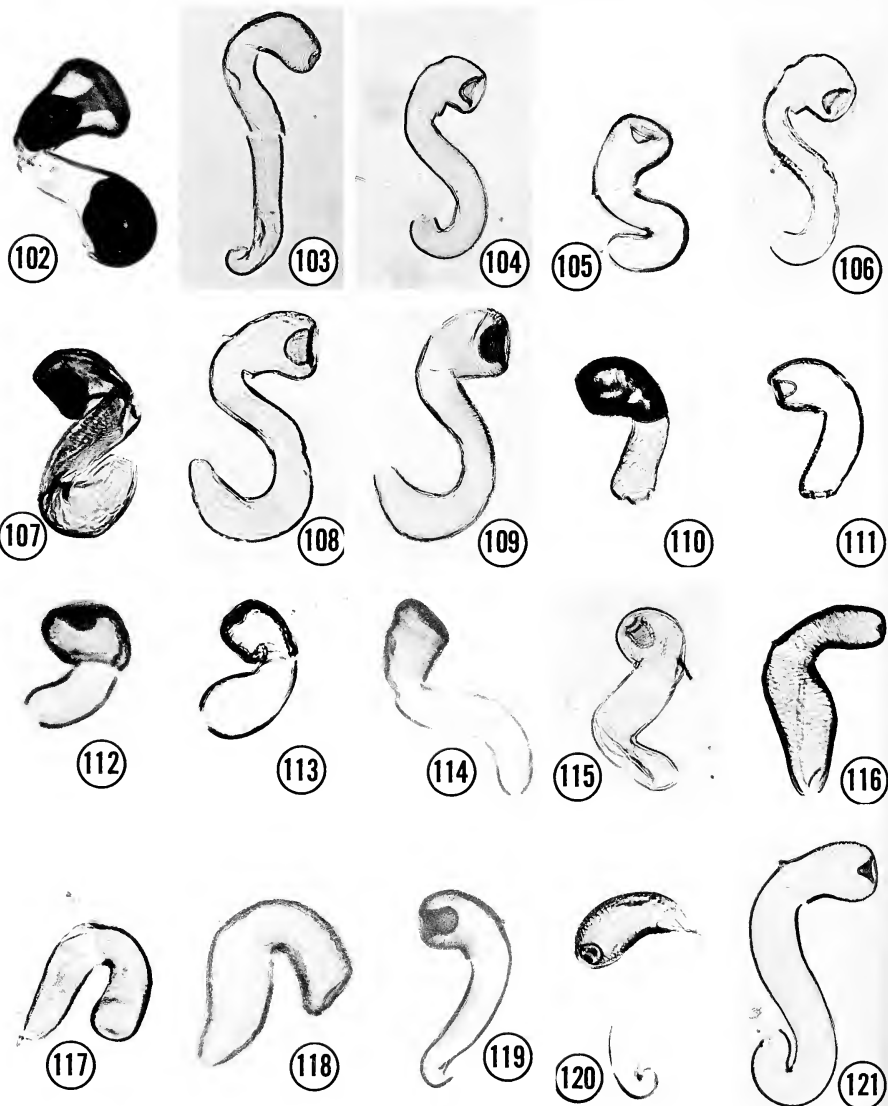
*Habitat.* Adults of this species have been collected from a liver trap, from the nest of a buzzard, and from the decaying carcass of a pig.

*Borboropora sulcifrons* (Casey)

Figs. 22, 101; Map 16

*Aneurota sulcifrons* Casey, 1893, p. 348 [type locality, Florida, Enterprise]; 1906, p. 252.





Figs. 102–121. Spermathecae of North American Falagriini. 102. *Cordalia obscura*. 103. *Falagriota occidua*. 104. *Myrmecocephalus cingulatus*. 105. *M. concinnus*. 106. *M. gracilis*. 107. *M. sculpturatus*. 108. *M. arizonicus*. 109. *M. gatineauensis*. 110. *M. caviceps*. 111. *M. pinalicus*. 112. *Falagria dissecta*. 113. *F. sulcata*. 114. *Falagrioma socorroensis*. 115. *Aleodorus partitus*. 116. *A. intricatus*. 117. *A. scutellaris*. 118. *A. bilobatus*. 119. *Lissagria laeviuscula*. 120. *L. laticeps*. 121. *Borboropora quadriceps*.

*Borboropora sulcifrons*; Fenyès, 1912, p. 25; 1920, p. 147; Leng, 1920, p. 124; Bernhauer and Scheerpeltz, 1926, p. 573; Seevers, 1978, p. 277.

*Diagnosis.* This species is readily recognized by its extremely minute body size.

*Description.* Length 1.35 mm. Body very minute; color rufo-brunneous to dark piceous; mouthparts and legs paler. Habitus as in Figure 22.

Head (Fig. 22) large, nearly quadrate, slightly longer than broad, lateral margins slightly arcuate, truncate at base, hind angles acutely rounded, prominent. Surface sparsely and minutely punctured and pubescent, strongly impressed along median line from middle of vertex to front. Eyes prominent, slightly shorter than length of temples. Antenna moderately short, feebly incrassate, not extending beyond anterior  $\frac{1}{3}$  of elytra. Prothorax nearly quadrate, much narrower than head, feebly convex, slightly longer than broad, broadest at anterior third; anterior angles broadly, evenly rounded; lateral margins rounded, moderately converging and straight to base; posterior margin broadly, evenly arcuate-truncate. Disc finely sulcate along median line except extreme apex, sulcus ending in a shallow, subbasal fovea. Surface moderately, minutely punctured and pubescent; surface between punctures smooth and shining. Scutellum flat, unmodified, densely punctured. Elytra with surface rather sparsely, evenly and minutely punctured and pubescent, except area of dense and coarse punctation near scutellum; surface between punctures smooth and shining. Abdomen broad at base, much narrower than elytra. Terga III–V shallowly, transversely impressed at base; impressions impunctate. Tergal surfaces moderately, minutely and asperately punctured and pubescent; surface between punctures smooth and polished.

*Male.* Eighth tergite with apical margin broadly arcuate at middle with comb of small denticles. Apical margin of eighth sternite broadly rounded. Median lobe of aedeagus as in Figure 101A. Paramere as in Figure 101B.

*Female.* Unknown.

*Type material.* *Aneurota sulcifrons* Casey. Holotype, in the Casey collection of the U.S. National Museum (Natural History), Washington, with the following labels: "prise [=Enterprise], .6 Fla. "/>CASEY bequest 1925/Type USNM 38928/"*Aneurota sulcifrons*."

*Distribution.* *Borboropora sulcifrons* is rarely encountered in North America. In addition to the type locality it is only known from one other locality in central Florida (Map 16). Cuban specimens have been examined that appear conspecific with those from Florida. Specimens have been collected in July.

*Material examined.* 1 specimen. UNITED STATES: *Florida*: Marion Co., Ocala, July (JHFC) 1.

*Habitat.* Little is known about the habitat of this species. One specimen at hand has been collected from a blacklight trap.

*Remarks.* Based upon only the two Casey descriptions of *Aneurota sulcifrons* (Casey, 1893, p. 348; 1906, p. 252), Scheerpeltz (1956) expressed the opinion that the European *Bohemiellina paradoxa* Machulka (1941) was identical with *A. sulcifrons*. Recently Smetana (1973), at the request of G. A. Lohse (Hamburg, West Germany), compared European material of *B. paradoxa* with the holotype of *Aneurota sulcifrons*, and "... proved beyond any doubt that *Bohemiellina* Mach. is a separate genus closely related to *Aneurota* Csy."

## UNRECOGNIZED SPECIES

*Falagria longicornis* Sachse, 1852, p. 116 [type locality, Georgia, U.S.A.].

*Falagria amabilis* Sachse, 1852, p. 116 [type locality, Georgia, U.S.A.].

I was unable to locate the type material of the above two species, and characters given in the original descriptions were not sufficient to confidently place them to genus in the Falagriini.

## PHYLOGENETIC ANALYSIS

Tikhomirova (1973) claimed that "Inadequate knowledge of the huge subfamily Aleocharinae, and the difficulty of diagnosing it, does not allow us to discuss in detail the kindred relationships within it. On this question it is only possible to put forward individual ideas" (translated from the Russian). Methods of phylogenetic analysis developed by Hennig (1966) are used here to produce a cladogram of probable phylogenetic relationships among the genera of the Falagriini. This analysis must remain tentative at present; with addition of taxa from other zoogeographic areas and the almost certain discovery of new taxa, details of this hypothesis will undoubtedly change.

Decisions of character polarity were determined by out-group comparison (Watrous and Wheeler, 1981). Representatives of genera of the tribe Sceptobiini (the putative sister group of the Falagriini), and of the genera *Oxypoda* (Oxypodae, Oxypodini), *Gnypeta* and *Tachyusa* (Tachysae, Oxypodini), and *Tachinus* (Tachyporinae) were selected to represent a taxonomic out-group. Members of the tribe Sceptobiini provide out-group comparisons from a closely related group, while the taxa chosen from the Oxypodini (Aleocharinae), and *Tachinus* (Tachyporinae) provide more distantly removed comparisons. Characters and their states are listed in Table 1. The proposed phylogenetic relationships among the genera of the Falagriini are summarized in a cladogram (Fig. 122).

Distribution of the following character states support the relationships hypothesized in the cladogram. The numbers in parentheses in the following paragraphs correspond to the numbers on the cladogram (Fig. 122) and in Table 1. References to illustrations of the apomorphic character states can be found by referring to Table 1.

**Head capsule.** In most Aleocharinae the head capsule does not have a defined neck. Among the Staphylinidae, a narrow neck is found in some Staphylininae (*Neobisnius*, *Erichsonius*), Xantholininae (most genera), and Paederinae (Dolicoanina). Members of the Falagriini have an extremely narrow neck (1), a condition that is regarded here as derived.

**Pronotum.** The pronotum varies greatly in form and convexity in the Falagriini. It is characterized by the presence of a median sulcus (3), and is appreciably narrowed behind the middle (5). Most Falagriini have the disc deeply sulcate (4) along the median line, except in *Cordalia* and *Falagriota* where the median sulcus is only faintly visible.

**Hypomera.** In the Falagriini the hypomera of the prothorax is exposed and generally visible in lateral aspect. In some taxa the hypomera is undelimited from the disc—a marginal ridge is absent (9) (Figs. 42, 43). Other Falagriini have the hypomera delimited from the disc by a marginal ridge or carina (Figs. 40, 41).

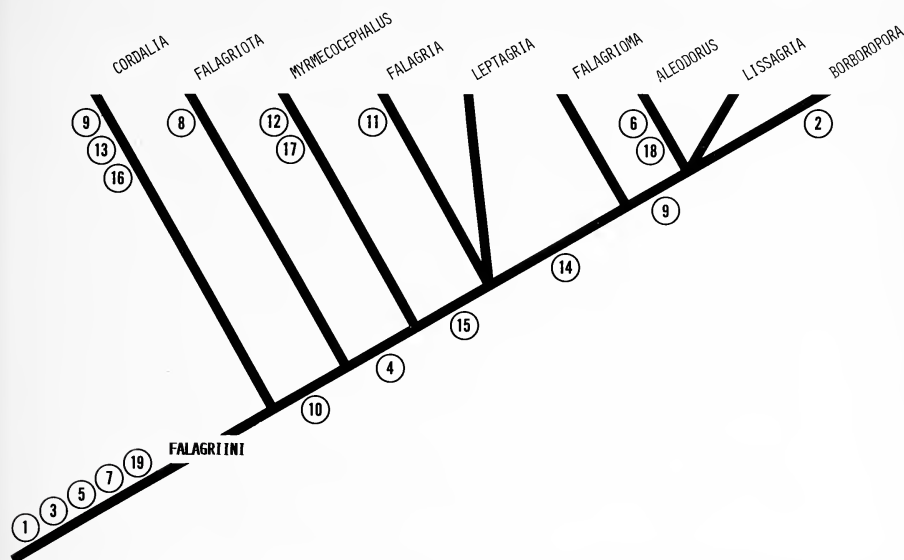


Fig. 122. Proposed phylogenetic relationships among the North American genera of the tribe Falagriini.

*Mesosternum.* The mesosternum (and its associated process) are on the same level or plane as the metasternum when viewed upside down. In *Aleodorus*, however, the mesosternum is on a level clearly above the metasternum (6) (Fig. 79), and the mesosternal process is very abbreviated and acute. In the majority of the Aleocharinae, the mesocoxae are set in deep acetabula conjointly formed by the meso- and metasterna; the acetabula are usually margined (Fig. 76). In the Falagriini (with the exception of *Cordalia*) the mesocoxae are not set in acetabula but are unmargined (10). Elsewhere in the Aleocharinae, unmargined acetabula occur in some termitophilous and myrmecophilous tribes (i.e., Corotocini and Dorylomimini).

*Mesospiracular peritremes.* In the Aleocharinae (and other Staphylinidae) the mesothoracic spiracles, which usually lie in unsclerotized membrane directly behind the front coxae, are surrounded by small, corset-like peritremes. In the Falagriini these peritremes are developed as enlarged plates which are usually heavily sclerotized and contiguous along the midline (7) (Figs. 79, 80). Among the Staphylinidae, enlarged peritremes also are found in the Tachyporinae (Tachyporini), Paederinae (Dolico-nina), Staphylininae (some Quediini), Aleocharinae (some Dorylomimini), Habrocerinae (*Nomimocerus*), Proteininae (*Megarthus* and *Metopsia*), and Trichophyi-nae (*Trichophya*).

*Scutellum.* The scutellum is generally unmodified in most Falagriini and other Aleocharinae. It is flattened to slightly convex, and coarsely punctured. In species of *Falagria* the scutellum is distinctly bicarinate, with two median, longitudinal carinae enclosing a smooth, depressed channel (11) (Figs. 35, 44). In *Myrmecocephalus* the scutellum is unicarinate with a broad basal carina not extending to the apex, or with a fine carina extending completely to the apex (12) (Fig. 34).



Table 1. Characters and character states used in the cladistic analysis of the North American Falagriini.

Character	Plesiomorphic	Apomorphic
1. Head capsule	Neck absent, or very broad	Neck very slender (Figs. 36, 39)
2. Head capsule	Rounded or transverse	Greatly enlarged, subquadrate (Figs. 21–22)
3. Pronotum	Not sulcate along median line	Sulcate along median line (Figs. 32–29)
4. Pronotum	Very faintly or obsoletely sulcate	Deeply sulcate (Figs. 34–39)
5. Pronotum	Not narrowed behind middle	Appreciably narrowed behind middle (Figs. 34–39)
6. Mesosternum	On same level or plane as metasternum; process generalized	On level or plane ventral to metasternum; process very short (Fig. 79)
7. Mesospiracular peritremes	Very small, corset-like	Greatly enlarged and contiguous, or nearly so, along midline (Figs. 79–80)
8. Mesospiracular peritremes	Peritremes large	Peritremes reduced, moderately small (Fig. 77)
9. Hypomera	Delimited from disc by marginal ridge or carina	Not delimited from disc by marginal ridge (Figs. 42–43)
10. Mesocoxal acetabula	Completely margined posteriorly by fine ridge	Not margined posteriorly, open
11. Scutellum	Unmodified	Bicarinate (Figs. 35, 44)
12. Scutellum	Unmodified	Unicarinate (Fig. 34)
13. Elytra	Unmodified	With depression at base near humeral angle
14. Elytral punctation	Uniform throughout	Dense and coarse near scutellum (Figs. 48–50)
15. Apical margin of tergum VIII	Unmodified, truncate	Arcuate at middle with comb of minute denticles (Figs. 72–75)
16. Apical margin of tergum VIII	Unmodified, truncate	Slightly emarginate, densely fimbriate (Fig. 70)
17. Integument	Without microsculpture	With transverse or reticulate microsculpture (Figs. 64, 67–69)
18. Male genitalia	Flagellum absent, or not highly coiled	Flagellum highly coiled (Figs. 94–97)
19. Male genitalia	Velum of paramerite and condylite confluent	Velum of paramerite and condylite clearly separated

*Elytral punctation.* Most Falagriini have uniformly and evenly punctured elytra. In species of the genera *Aleodorus*, *Falagrioma*, *Borboropora*, and *Lissagria* the elytra are very coarsely and densely punctured near the scutellum (14) (Figs. 48–50). Elsewhere in the subfamily, this condition is not known to occur.

*Tergum VIII.* Most species of Falagriini have the apical margin of the eighth tergite unmodified (truncate or arcuate-truncate) in both sexes. Species of *Falagrioma*, *Aleodorus*, *Borboropora*, *Lissagria*, *Falagria*, and *Leptagria* have a distinct comb of minute denticles on the arcuate portion of the apical margin (15) (Figs. 72–75). *Cordalia obscura* has the apical margin of the eighth tergite slightly emarginate and densely fimbriate (16) (Fig. 70).

*Integumental sculpture.* The majority of Falagriini have a smooth and polished integument between punctures. All species of *Myrmecocephalus* (except *arizonicus*) have transverse or reticulate microsculpture on portions of the integument (17) (Figs. 65, 67–69), a feature unique among known North American Falagriini.

*Median lobe of aedeagus.* Undoubtedly, most of the characters useful for deducing relationships in this tribe are found in the median lobe of the aedeagus. However, most of the accessory structures (spinules, denticulate plates, etc.) of the internal sac cannot be homologized at this time. A uniquely and highly convoluted flagellum is found in species of *Aleodorus* (18) (Figs. 94A–97A) and not elsewhere in the tribe.

*Paramere of aedeagus.* As in other Aleocharinae, the relatively large parameres articulate with condyles distal to the median foramen of the median lobe, and each is comprised of two parts, the condylite and paramerite. The velum (probably unique to the Aleocharinae) is a distinctive element of the parameres; the condylite velum is usually confluent with the paramerite velum. However, in the Falagriini and Sceptobiini the condylite velum is clearly separated from the paramerite velum (19).

The tribe Falagriini is characterized by the synapomorphic features of: slender neck of the head capsule (1), presence of a median sulcus of the pronotum (3), appreciably narrowed pronotum behind the middle (5), usually enlarged mesospiracular peritremes (7), and separation of the velum of the paramerite and condylite of the paramere (19). The last of these apomorphic features (19) is found only in one other group, the tribe Sceptobiini, which may prove to be the sister group of the Falagriini. Some of the above apomorphic characters (i.e., 1, 7) are shared also by other staphylinid taxa (as discussed earlier), but are considered parallel developments in these groups rather than indicative of relationship.

The following cladistic analysis of the genera of the North American Falagriini has one multiply derived character state and one character reversal. In this hypothesis (Fig. 122), *Cordalia* stands as the sister of all other falagriine genera. The apomorphic features unique to *Cordalia* are the presence of a deep depression at the base of the elytra near the humeri (13), and the densely fimbriate apical margin of the eighth tergite (16). An additional apomorphic feature that supports *Cordalia* is the unlimited hypomera of the prothorax (9), which is also shared with some other falagriine genera (i.e., *Aleodorus*, *Lissagria*, and *Borboropora*). The sister group of *Cordalia* is supported by the unmarginated posterior aspects of the mesocoxal acetabula (10). The genus *Falagriota* is recognized by the reduced mesospiracular peritremes (8), here regarded as a character reversal. The sister lineage of *Falagriota*, comprised of the genera *Myrmecocephalus*, *Falagria*, *Leptagria*, *Falagrioma*, *Aleodorus*, *Lissagria*, and

*Borboropora*, is based on the deeply sulcate pronotum (4). Species of *Myrmecocephalus* have a unicarinate scutellum (12), and an integument usually with transverse or reticulate microsculpture (17). The lineage of *Falagria*, *Leptagria*, *Falagrioma*, *Aleodorus*, *Lissagria*, and *Borboropora* is supported by the presence of a comb of denticles on the apical margin of the eighth tergite (15). Species of *Falagria* are recognized by the bicarinate scutellum (11), a feature not found elsewhere in the Falagriini. *Leptagria* is not supported by any apomorphic characters. The lineage of *Falagrioma*, *Aleodorus*, *Lissagria*, and *Borboropora* is founded on the presence of an area of dense, coarse punctation on the elytra adjacent to the scutellum (14). *Falagrioma* cannot be supported or recognized by an apomorphic character. The lineage of *Aleodorus*, *Lissagria*, and *Borboropora* is supported by the undelimited hypomera of the prothorax (9), an apomorphic feature shared also with *Cordalia*. The mesosternum of species of *Aleodorus* is in a plane ventral to the metasternum (6), and the internal sac of the male genitalia has a highly coiled flagellum (18), both considered uniquely derived in this lineage. Unlike *Aleodorus*, *Lissagria* and *Borboropora* have the meso- and metasternum on the same level. Both genera lack a convoluted flagellum. *Borboropora* has an extremely enlarged and subquadrate head capsule which is usually longitudinally impressed along the median line and sometimes excised at the occiput (2). *Lissagria* is a branch of an unresolved trichotomy, and is not supported by an apomorphic character.

#### ACKNOWLEDGMENTS

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BROOD VI OF 17-YEAR PERIODICAL CICADAS,  
*MAGICICADA* SPP. (HEMIPTERA: CICADIDAE):  
NEW EVIDENCE FROM CONNECTICUT, THE  
HYPOTHETICAL 4-YEAR DECELERATION,  
AND THE STATUS OF THE BROOD

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*Abstract.*—Small emergences of the 17-year periodical cicada, *Magicicada septendecim* (L.), occurred in central Connecticut during 1983. An adult wing and two nymphal exuviae were collected at one site, and the intermittent singing of one to four males was heard at four other localities. The density estimated at one site was only one adult per hectare. Females apparently did not oviposit during 1983. At every locality visited during 1983, there was ovipositional damage caused by females of the sympatric Brood II, which emerged in abundance during 1979. Evidence obtained in 1983 and 1932 (51 years earlier) suggests collectively that Brood VI is not a self-reproducing brood in Connecticut. It is proposed that emergences of Brood VI may be attributed to a few adults of Brood II, which underwent a 4-year deceleration in nymphal development.

A critical examination of early distributional records for Brood VI indicates that the evidence is ambiguous. Misidentifications, developmental flexibility of 17-year periodical cicadas, and records of 13-year cicadas may account for most of the records of Brood VI in the eastern United States. The 4-year deceleration proposed here may be one factor that has contributed to the ambiguity of records of Brood VI and possibly to the formation of cicada broods.

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How the many allochronic broods of 13- and 17-year periodical cicadas, *Magicicada* spp., evolved from their ancestral brood(s) is an intriguing question that has stimulated much research. Alexander and Moore (1962), Lloyd and Dybas (1966b), Lloyd and White (1976), and others have hypothesized that the modern broods of periodical cicadas may have originated by 1- or 4-year aberrations in the length of the life cycle. There is evidence that some periodical cicadas have undergone a 4-year acceleration, a 1-year acceleration, or a 1-year deceleration in their developmental time. Dybas (1969) has documented a 4-year acceleration in a portion of the 17-year Brood XIII in the Chicago area. Marlatt (1907, p. 24) has stated that one of his correspondents witnessed a 1-year acceleration of cicadas enclosed in a greenhouse. A 1-year deceleration in development has recently occurred in many *Magicicada* nymphs of Brood XIV in Kentucky (White and Lloyd, 1979). In this paper, I suggest that the cicadas observed in Connecticut during 1932 and 1983 underwent a 4-year deceleration in their nymphal development.

Connecticut is an excellent location for observing unscheduled emergences because only Broods II and XI have been well-documented there (e.g., Marlatt, 1907). Since the nineteenth century, Brood XI has declined rapidly, and it is now apparently

extinct because no adults emerged in 1971 (Manter, 1974). By contrast, the large Brood II has appeared during every scheduled emergence in the twentieth century, most recently in 1979 (Britton, 1912, 1928; Friend, 1946; Leonard, 1964; Maier, 1982a, b). This brood, which in Connecticut has only the species *M. septendecim* (L.), continues to thrive at several localities (Maier, 1980, 1982a, b).

The unexpected emergence of periodical cicadas during 1983 has led to a reexamination of Connecticut collections and literature for overlooked records of Brood VI, which should have emerged in 1983. The search has revealed a record of an emergence 51 years earlier (Anonymous, 1932, p. 232). Unfortunately, this report of Brood VI in the monthly record is omitted from an annual summary and a map of the distribution of Brood VI (Anonymous, 1932, p. 424 and fig.). Britton (1933) corroborated this first report by stating that his staff in Connecticut had collected a few periodical cicadas during 1932. Strangely, he concluded that these adults probably belonged to Brood VII, which was due to emerge in 1933.

The scarcity of adults in 1932 and 1983 suggests that Brood VI does not exist as a self-reproducing brood in Connecticut. Here I propose that these cicadas are actually 21-year-old representatives of Brood II. My hypothesis of a 4-year lengthening of nymphal development will be discussed in relation to hypotheses of brood formation and to the status of Brood VI.

#### METHODS

In June 1983, five sites in Connecticut were surveyed for the presence of adults and for the egg-laying scars of females. One location in each town of Southington (Hartford Co.), Middlefield (Middlesex Co.), North Branford, Guilford, and Hamden (New Haven Co.) was surveyed for approximately 2 hr per visit. Guilford was inspected on 7 to 9 June and on 15 to 20 June, and the remaining towns were checked once between 9 and 14 June.

Adult density at Southington was estimated on 9 June in the same deciduous forest where Maier (1980, 1982b) recorded the density of Brood II nymphs in 1978 and adults in 1979. To approximate density, the number of singing males was doubled to account for non-singing females; and, this total was divided by the area within the hearing range of the listener. Hearing range was determined by walking away from a singing male until that individual could no longer be heard. The accuracy of the estimate was checked by having two listeners at each location and by using four locations in the forest.

Insect collections housed at The Connecticut Agricultural Experiment Station (New Haven), the Peabody Museum (New Haven) the University of Connecticut (Storrs), and Clemson University (Clemson, South Carolina) were examined for additional specimens collected during the emergence years of Brood VI. All Connecticut specimens collected during 1932 or 1983 are now located in the insect collection of The Connecticut Agricultural Experiment Station.

#### RESULTS

Adults of *M. septendecim* emerged at each site examined during 1983 (Fig. 1). Two nymphal exuviae (one male, one female) and one adult wing collected in a North Branford yard constituted the physical evidence of the 1983 emergence. The yard

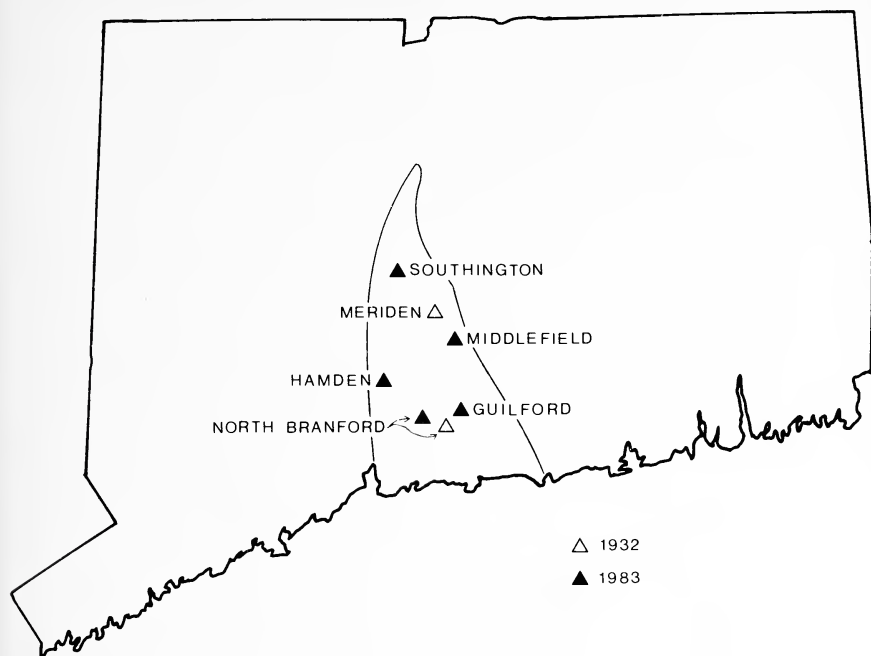


Fig. 1. Distributional records of *Magicicada septendecim* from Connecticut for 1932 and 1983. Each symbol indicates where adults were collected or heard during 1932 ( $\triangle$ ) or where singing or exuviae were recorded during 1983 ( $\blacktriangle$ ). The line encircling the symbols delimits the distributional range of Brood II (modified from Maier, 1982b).

owner, an entomologist, stated that he had struck a live adult and its nymphal exuviae while he was mowing grass on 2 June. A search on 9 June produced the physical evidence to document his observation.

One to four males of *M. septendecim* were singing intermittently at each of the other sites surveyed between 7 and 18 June (Fig. 1). At Guilford, the acoustical records represented three males on 7 June, four males on 8 June, one male on 9 June, three males on 15 June, and one male on 18 June. During each visit between 7 and 15 June, a male was singing in the top of the same sugar maple, *Acer saccharum* Marsh. The number of males heard on 9, 10, or 14 June totaled three at Southington, one at Middlefield, and two at Hamden. The density of adult cicadas at Southington was approximately one per hectare.

Females that emerged during 1983 did not cause any recognizable oviposition damage. However, oviposition scars from 1979 were evident at each of the five sites at which a 1983 emergence of *M. septendecim* was recorded.

Additional records for Marlatt's (1898a) Brood VI were obtained from the insect collection at The Connecticut Agricultural Experiment Station. The collecting dates (20 and 23 June 1932), the location (North Branford), and the collectors (M. Zappe and N. Turner) listed on the labels indicated that these specimens represented most of those upon which Britton (1933) had based his report of a 1932 emergence. In



all, there were ten specimens, including four males, four females (one had a fungal infection of *Massospora*), and two without abdomens. The 1932 collection site in North Branford is located 3 km away and equidistant from the 1983 emergence sites in North Branford and Guilford (Fig. 1).

#### DISCUSSION

*Hypothetical 4-year deceleration.* Periodical cicadas that emerged in Connecticut during 1932 and 1983 would be assigned conventionally to Marlatt's (1898a) Brood VI. A typical emergence of Brood VI in the northeastern United States consists of only a few adults (Anonymous, 1932; Hopkins, 1900; Marlatt, 1907). Successful reproduction by sparse populations of adults seems unlikely because small populations of periodical cicadas are usually annihilated by predators (Alexander and Moore, 1962; Chilcote and Stehr, 1984; Karban, 1982; Lloyd and Dybas, 1966a, b). Therefore, I propose that the scarce adults of "Brood VI" from Connecticut actually represent 21-year-old stragglers of the large sympatric Brood II, the only other extant brood in the state. Interestingly, White and Lloyd (1975) did find 19-year-old nymphs in the soil after a major emergence of Brood X in Ohio. If these cicadas survived for two more years, they could have emerged synchronously with the adults of Brood XIV. It is possible, then, that a 4-year deceleration in nymphal development may be responsible for other records of sparse populations.

An alternative hypothesis would be that Connecticut populations of Brood VI are indeed self-reproducing ones, which have dwindled greatly in size due to past 4-year accelerations of members to Brood II. That is, populations of "Brood VI" have reached Lloyd and White's (1976) "phase three." Two problems cast doubt upon this alternative interpretation. First, as mentioned above, successful reproduction by exceedingly small populations is unlikely. This suggestion can be evaluated in 1996 when a sparse population of Brood II is scheduled to emerge at the northernmost Connecticut site recorded by Maier (1982b). At present, however, the rapid demise of Brood XI in Connecticut (e.g., Manter, 1974) serves as a vivid reminder of the fate of a small or local population of *M. septendecim*. Second, given the more than 3 centuries of entomological activity in Connecticut and the possible self-reproduction of this brood, it seems odd that only two emergences of Brood VI have ever been detected in the state.

Hypothetical 4-year decelerations in nymphal development may have contributed to the formation of some of the 17-year broods. For example, let us examine the Broods I and XIV on Long Island. Simon and Lloyd (1982) have hypothesized that Brood XIV is derived from Brood I by 1- and 4-year accelerations (i.e.,  $XIV \rightarrow X \rightarrow IX \rightarrow V \rightarrow I$ ). Their hypothesis requires four steps whereas the derivation of Brood I from Brood XIV by a 4-year deceleration would require only a single step. Simon and Lloyd (1982) have apparently rejected the possibility of a 4-year deceleration of some members of Brood XIV in favor of a more complex scheme because they had seen no examples of 4-year decelerations and because they had Long Island records for all the broods in their evolutionary scenario. However, their single Long Island record of Brood IX is based on correspondence (Davis, 1920) and therefore must be considered questionable. Moreover, only the abundant Brood XIV and the less abundant Broods I and X are recently well-documented on Long Island. Given the pro-

posed developmental flexibility of 17-year cicadas, I offer the alternate hypothesis that Brood XIV may have produced populations of Broods I and X by 4-year decelerations and accelerations, respectively.

The current theory of brood formation advanced by Lloyd and White (1976) and others draws heavily upon the distributional records summarized by Marlatt (1907). Many of Marlatt's (1907) records are probably ambiguous or erroneous, as I shall demonstrate shortly. Given the apparent developmental repertoire of periodical cicadas, it seems absolutely essential to rely solely upon unambiguous records to support a general theory of brood formation. Consideration of only the unequivocal evidence will surely reduce the number of self-reproducing broods and drastically decrease the distributional range of others.

*Status of Brood VI.* The question of the validity of Brood VI has concerned Walsh and Riley (1868), Marlatt (1898b), and other students of cicada biology. Distributional data published by the Insect Pest Survey (Anonymous, 1932) and Marlatt (1907) show that Brood VI has the widest range of any 17-year brood. An examination of the evidence, however, indicates that most of the records could be attributed to other broods (e.g., Lloyd et al., 1983; Stannard, 1975) or to other species of cicadas (e.g., Moore, 1966). Fundamental problems with much of the early distributional data are that the limits of 13- and 17-year broods were not fully understood, the variation in the duration of the life cycle was not recognized very often, the species were not identified, and most of the observations were not corroborated with specimens deposited in museums.

Many of the ambiguous records of Brood VI are based on observations conducted in 1881 (Riley, 1881), 1898 (Hopkins, 1900; Marlatt, 1898b, c; Schwarz, 1898), and 1932 (Anonymous, 1932). In the first two years, emergences over large areas could also be attributed to the major 13-year broods that emerged during 1881 (Brood XIX) and 1898 (Brood XXIII). Thirteen-year cicadas of Brood XIX, which underwent a 4-year deceleration in nymphal development, could have emerged during 1898; but, they would have appeared in different areas than would have members of Brood XXIII. Lloyd et al. (1983) and Stannard (1975) have suggested that all Illinois records of Brood VI belong to other broods, such as Brood XXIII. Lloyd et al. (1983) have hypothesized that the 1898 records of Brood VI were actually those of new populations of Brood XXIII, which only became distinguishable as new populations 30 years after members of the "grandparental broods" (X and XIX) hybridized in 1868. Periodical cicadas that emerged in Georgia and the Carolinas during 1932 (Anonymous, 1932) may have been Brood XIX members that accelerated development by 1 year, (Alexander and Moore, 1962), Brood X members that accelerated development by 4 years, or even Brood II members that decelerated development by 4 years.

Outside the distributional range of 13-year broods, records of Brood VI are probably derived mainly from 18-year-old stragglers of Brood V, 21-year-old stragglers of Brood II, or 13-year-old members of Brood X. During each scheduled emergence of Brood VI, 1-year stragglers of Brood V would also have appeared in West Virginia and bordering states. Even though Marlatt (1898c) and Schwarz (1898) recognized that Brood V stragglers probably accounted for many of the Brood VI records, Marlatt (1907) still included these questionable records in his monograph. Continual sympatry of two self-reproducing broods separated by 1 year seems very improbable in

light of recent analyses (Alexander and Moore, 1962; Lloyd and Dybas, 1966b; Lloyd and White, 1976; White and Lloyd, 1979). Clearly, most of the Brood VI records from within the range of Brood V (e.g., Hopkins, 1900) should be assigned to the latter brood. Records of Brood VI from Wisconsin, Indiana, Ohio, Pennsylvania, New York, New Jersey, Maryland, and Virginia could have resulted from 4-year accelerations of Brood X, 4-year decelerations of Brood II, or both. In particular, most of the records of Brood VI from southwestern Wisconsin, northern Indiana, and northwestern Ohio are from counties where Brood X is also recorded (e.g., Anonymous, 1932, 1936; Marlatt, 1907). Similarly, Brood VI emergences in New York, Pennsylvania, and New Jersey tend to be located in counties where Brood II, X, or both have been recorded (e.g., Marlatt, 1907; Simon and Lloyd, 1982).

Convincing evidence of a self-reproducing Brood VI should satisfy the following requirements: (1) An emergence should consist of one or more populations that reproduce successfully. (2) An emergence site should be separated geographically from sites where major broods are scheduled to emerge in the same year or within 1 to 4 years. (3) Adults should emerge at the same location during at least two consecutive emergences. (4) Specimens from each of these consecutive emergences should be deposited in a major insect collection. To date, no published record of Brood VI meets all of these criteria. However, there are intriguing reports of large emergences in 1898 (Marlatt, 1898b) and 1932 (Anonymous, 1932). Sizeable emergences that were reported from Michigan and Wisconsin may have been those of adults of *Okanagana* spp. (Moore, 1966; A. Young, pers. comm., 1983) which resemble adults of *Magicicada* spp. Specimens of *M. septendecim* (one from 1915, six from 1949) collected in three Wisconsin counties are deposited in the collection at the University of Wisconsin at Madison (S. Krauth, pers. comm., 1984). Unfortunately, neither the Wisconsin records nor the Michigan ones completely satisfy criteria 3 and 4.

Large emergences recorded in the Carolinas and Georgia (e.g., Anonymous, 1932; Marlatt, 1907) have occurred in counties located within 200 km of the point where North Carolina, South Carolina, and Georgia meet. These areas seem to be the most promising locations for finding populations of Brood VI, which will meet all of the above requirements. A 1932 emergence in Oconee County, South Carolina is documented with a large series of specimens, which are housed at Clemson University. Because these cicadas emerged within the distributional range of Brood XIX, they were originally identified as *M. tredecim* (Walsh and Riley) adults that had accelerated their development by 1 year (Alexander and Moore, 1962). However, a 1983 emergence documented with two adult females and one nymphal exuviae (examined by me), several reports of large emergences in 1966 (Gorsuch, pers. comm., 1983), and an emergence record from 1881 (Alexander and Moore, 1962) now suggest that the populations in Oconee County may be representatives of a self-reproducing Brood VI. Analyses of wing morphology (Simon, 1983) may provide a means to determine whether these specimens belong to a 13- or 17-year brood. Finally, M. Lloyd (pers. comm., 1984) and C. Simon (pers. comm., 1984) have indicated that they are presently studying self-perpetuating populations of Brood VI in North Carolina. Voucher specimens of *M. septendecim* and *M. septendecula* (Alexander and Moore) from a 1983 emergence in North Carolina are deposited in the collection at North Carolina

State University in Raleigh (C. Parron, pers. comm., 1983). The adults of *M. septendecula* represent the first voucher specimens of this species for Brood VI.

Marlatt's (1907) suggestion that Brood VI is "an assemblage of swarms of diverse origin" has yet to be disproven. Certainly, most of the records from northern states can be attributed to other broods. Records from southern states may prove to be valid ones of Brood VI, but convincing evidence of their authenticity is presently wanting. Ongoing distributional studies (e.g., T. Moore, pers. comm., 1984; C. Simon, pers. comm., 1984) conducted in conjunction with morphometric and enzymic analyses (e.g., Simon, 1979, 1983) may ultimately answer questions about the validity of Brood VI.

#### ACKNOWLEDGMENTS

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## THE NATURAL HISTORY OF *ONCOCNEMIS PIFFARDI* (WALKER) (LEPIDOPTERA: NOCTUIDAE)<sup>1</sup>

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*Abstract.*—The natural history of *Oncocnemis piffardi* (Walker) is described and the larva and pupa are illustrated. Larvae have been field-collected as well as cultured on *Spiraea latifolia* (Art.) Borkh., its natural host. *Elpe semiothisae* (Brooks) (Tachinidae) and an apparently undescribed *Mesocharus* (Ichneumonidae) were reared from field-collected larvae. The *Mesocharus* is a hyperparasite of yet another ichneumonid.

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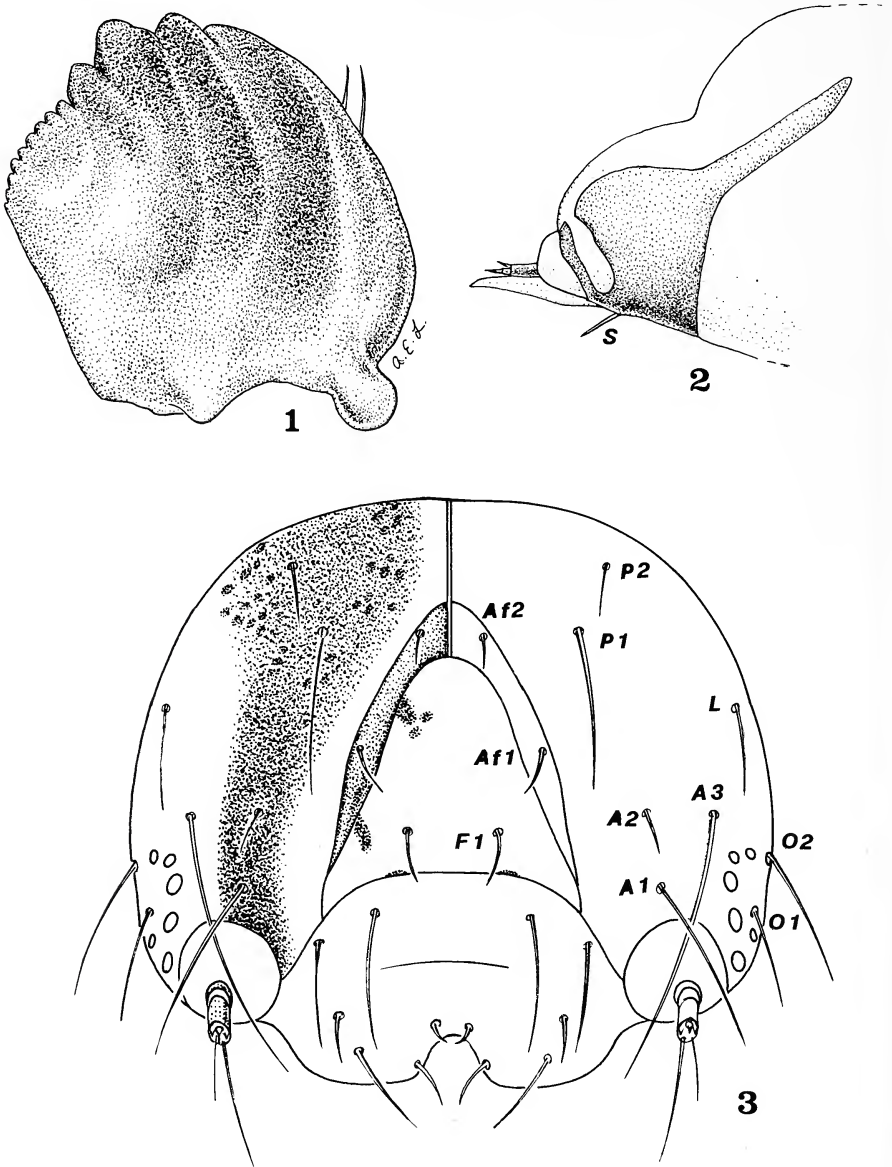
In 1978, I attempted to identify the host of *Oncocnemis piffardi* (Walker, 1862) by providing newly eclosed larvae an assortment of the most common plants in their environs, the Adirondack Mountains near Indian Lake, New York. The larvae had hatched from ova obtained from a female from the previous summer; ova overwinter in this species. When the larvae failed to feed on the first dozen plants provided, another dozen different species were made available. This process was repeated until over 100 different plants had been provided. The only acceptable host discovered was *Spiraea latifolia* Ait. (Borkh.) (Rosaceae), but by the time this was evident the few surviving first-instar larvae were so impoverished that they succumbed to disease.

Having established *S. latifolia* as a host, I revisited my collecting site in 1979 and searched *Spiraea* stands in June, when larvae should have been nearly full grown. At that time several acres of *Spiraea* had been defoliated by *O. piffardi* and larvae were much in evidence on the bare stems of *Spiraea*. Unfortunately, I had to spend the following 2 months in another state and it wasn't until 1980 that I continued field work in the Adirondacks. In 1980, the numbers of *O. piffardi* had decreased dramatically but larvae could still be found shortly after dusk with the aid of a lantern. A larva habitually rests with its body held parallel to the main stem, frequently choosing a dead or denuded vertical twig. Adults were obtained in the laboratory by rearing the nearly grown wild-caught larvae on fresh *Spiraea* leaves. Two additional adults found feeding on composite blossoms were taken at dusk. One moth was nectaring on Joe-Pye-Weed, *Eupatorium purpureum* L., and the other was on *Aster umbellatus* Mill.

Two wild-caught larvae had been parasitized. One of the parasites was *Elpe semiothisae* (Brooks) (Diptera: Tachinidae) which was previously known to be a parasite of geometrid and tortricid larvae (Sabrosky, 1975). Also, an apparently undescribed *Mesocharus* wasp (Ichneumonidae) was obtained. It was a hyperparasite of yet another ichneumonid wasp judging from the size and contents of an associated ichneumonid cocoon.

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Figs. 1-3. 1. Oral face of left mandible. 2. Hypopharyngeal complex. 3. Head capsule, frontal view.

#### ULTIMATE INSTAR LARVA

*General* (Fig. 4). Head 2.6 mm wide (N = 14); total length 35.0 mm (fully-distended, preserved larvae). Abdominal prolegs present on 3rd through 6th and 10th



Fig. 4. *Oncocnemis piffardi*, last instar larva, Adirondack Mountains, New York.

segments. Body protuberant on A-8; prothoracic shield with a pair of prominent longitudinal stripes.

*Coloration* (living material). Head and body gray; head with midfrontal black band which continues onto prothoracic shield; body with slight rufous tinge along mid-dorsal line; sides striated with various shades of gray; subventricular line white for anterior half of body, fading to gray posteriorly.

*Head* (Fig. 3). Epicranial suture 1.2 times height of frons; 2nd adfrontal seta (Af2) posterior to apex of frons; pigmented band present from lower region of head to vertex, but interrupted by antennal base; ocellar interspaces between Oc1 and Oc2 equal to diameter of Oc2; Oc2 to Oc3 equal to one-half diameter of Oc3; Oc3 to Oc4 equal to diameter of Oc3; Oc4 to Oc6 approximately twice diameter of Oc4; Oc4 to Oc5 approximately twice diameter of Oc4.

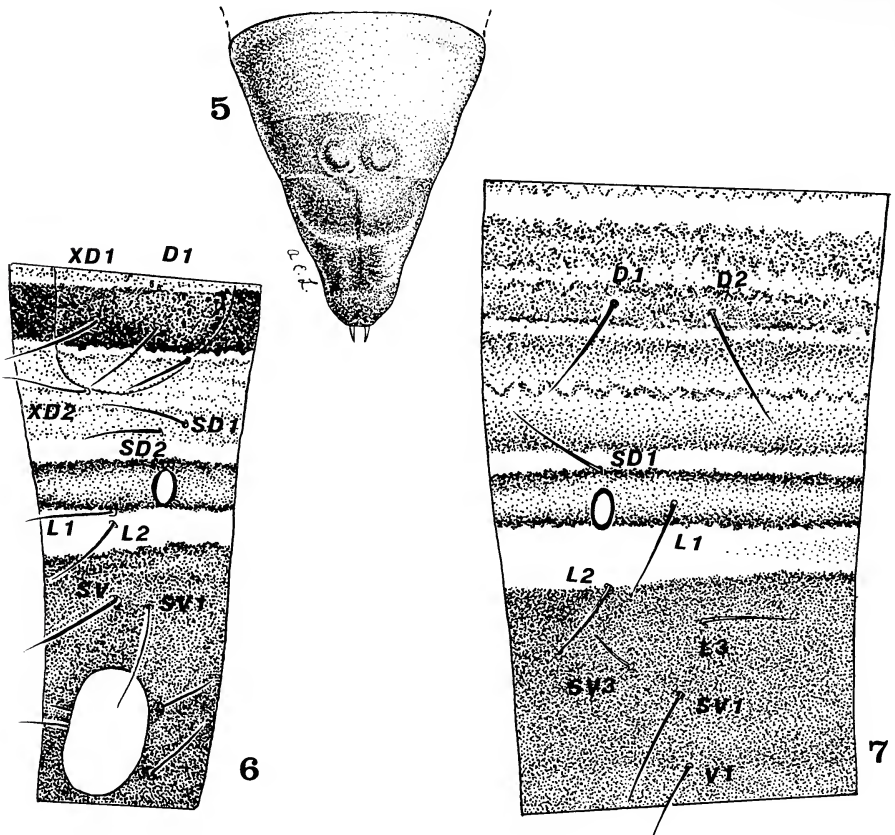
*Mouthparts. Hypopharyngeal complex* (Fig. 2). Spinneret with distal lip surpassing second segment of labial palpus, bare; Lp3 1.5 times length of Lp2; stipular setae (S) subequal in length to Lp's, including seta; distal, proximomedial and proximolateral regions of hypopharynx all lack setae; labrum with median notch.

*Mandible* (Fig. 1). With sixth tooth of 8-9 low subteeth; oral face with 3 shallow ridges, no basal tooth.

*Prothorax* (Fig. 6). With a pair of prominent black subdorsal stripes; narrow spiracular band present in living material, but fades when preserved; prothoracic setae as illustrated.

*Abdominal segments.* Ab-1 (Fig. 7) with primary setae as shown; Ab2-8 similar,





Figs. 5-7. 5. Pupal cremaster. 6. First thoracic segment. 7. First abdominal segment.

Ab-8 with a low pair of dorsal protuberances; Ab9 and 10 slope sharply downwards giving an outline characteristic of *Oncocnemis* species.

*Crochets*. Uniordinal, 18-25 per 3rd proleg; 18-27 per 4th, 21-31 per 5th, 26-33 per 6th, and 22-32 for the anal proleg (N = 14).

*Pupal cremaster* (Fig. 5). Terminating in a pair of heavy spines.

*Material examined*. 14 specimens, 6 miles east of Indian Lake, 555 meters, lat. 43.45.30 long. 74.10.14, Hamilton Co., New York, determined and reared by T. L. McCabe. Cultures are coded tlm 80-59, 80-124, and 80-184.

#### DIAGNOSIS

The dorsal hump on Ab-8 of the larva is apparently not evident in other previously reported *Oncocnemis* larvae (Crumb, 1956), although I have seen it in *Oncocnemis figurata pallidior* Barnes (reared on *Symphoricarpos occidentalis* Hooker) and in the closely related *Apharetra purpurea* McDunnough, *Sympistis melaleuca* (Thunberg),

and *Homohadena badistriga* (Grote). The pupal cremaster of *O. piffardi* differs very little from that of *Homohadena badistriga*; terminal spines are not as heavily chitinized.

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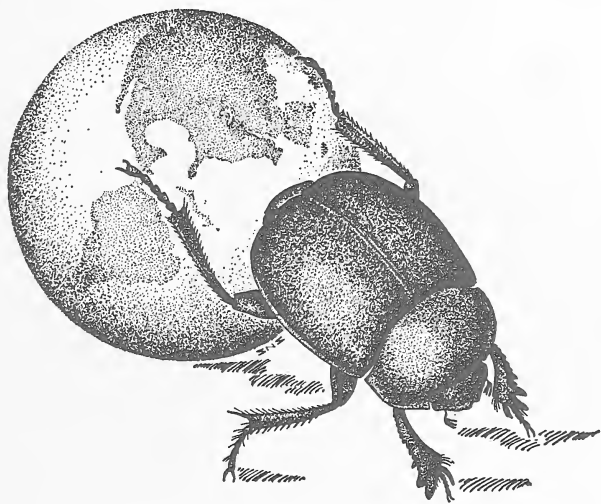
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## MALE TERRITORIAL BEHAVIOR IN FOUR SPECIES OF THE TRIBE CER CERINI (SPHECIDAE: PHILANTHINAE)

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**Abstract.**—Males of four species of Cercerini have been found to defend territories and to scent-mark stems on the peripheries of the territories: *Eucerceris flavocincta*, *E. cressoni*, *E. superba*, and *Cerceris nigrescens*. Males of *E. flavocincta* form aggregations resembling leks in which large males are more likely to maintain possession of a territory because of their advantage in aggressive interactions. Data are also presented on nest distribution and prey of these species.

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Males of most species of Philanthinae possess hair brushes on the clypeus associated with the aperture of their large mandibular glands; the same species also possess varied patterns of hairs on the venter of the abdomen. Males of many of these species are known to be territorial and, via a behavior referred to as "abdomen dragging" (Alcock, 1975a), probably scent-mark grass stems on the margins of their territories. Recently, it has been confirmed that volatile chemicals originating in the mandibular glands are applied to stems by territorial males of *Philanthus* (Schmidt et al., 1985). It is thought that the pheromones are applied to the stems with the clypeal hair brushes and subsequently spread with the abdominal hairs as they come into contact with the marked portion of the stem as the male walks forward (Gwynne, 1978). Evidence suggests that the pheromone is attractive to females, as most matings that have been observed occur within territories (e.g., Gwynne, 1980; O'Neill, 1983b).

In the tribe Cercerini, the clypeal hair brushes are shorter and directed downward, as compared to *Philanthus*, where they are directed toward the midline. Also, the abdominal hairs tend to be poorly developed or, as in many *Eucerceris*, confined to bands on one or more sternites. Territoriality and scent-marking have been less frequently reported in the Cercerini than in *Philanthus*. Steiner (1978) described an aggregation of male *Eucerceris flavocincta* in Oregon in which individuals were territorial for short periods, and Alcock (1975b) reported briefly on territoriality and scent-marking in *E. arenaria* Scullen, *E. canaliculata* (Say), *E. rubripes* Cresson, and *E. tricolor* Cockerell from localities in Arizona and New Mexico.

In this paper we report on four species of Cercerini observed in Colorado: *Eucerceris flavocincta*, *E. cressoni*, *E. superba*, and *Cerceris nigrescens*.

### RESULTS

#### *Eucerceris flavocincta* Cresson

An aggregation of males was discovered in mid-July 1979 in an intermountain valley known as Stove Prairie, 45 km west of Fort Collins, Colorado, at an altitude of 2,200 m. Males occupied a rocky outcrop adjacent to a grove of ponderosa pines and juniper. Males were abundant on this same outcrop in July 1981 and again in



July 1982, when most of our studies were made. The number of territories on the outcrop varied from four to about 20 on various days, with a total of 30 different territories identified in 1982. In addition, there were a few isolated territories in a meadow 100 m or more from the outcrop. These occurred in bare spots surrounded by grasses and weeds and were mostly widely spaced, at least several meters apart. In contrast, territory density at the outcrop was much higher. For example, 17 territories occupied on 22 July 1982 were only 1.5 m apart on average ( $SD = 0.7$ ; range = 1.0 to 4.0).

Behavior of males on territories consisted primarily of orienting to and pursuing passing insects and aggressive interactions with conspecific males. Males perched on rocks or low branches of trees or bushes, assuming an "alert" posture, with the head tilted slightly upward, the antennae held rigidly forward or upward, and the wings held obliquely upward (as illustrated by Steiner, 1978). Males frequently moved the head slightly or rotated their entire body to face in a different direction. Flights from perches were frequent (mean = 6.4/min;  $N = 76$  for 5 individuals) and of two kinds: slow circling flights over a radius of about a meter from the perch, often appearing "exploratory," but sometimes leading to scent-marking; and very swift, straight flights, sometimes two or more meters in length and sometimes in obvious pursuit of another insect. While pursuing insects of other species, particularly syrphid flies, which were common here, the territory resident followed behind and below, without making contact. However, interactions with conspecific males were quite different in form. When a conspecific male flew close by, the result was pursuit and often a tight "swirling flight" (Alcock, 1975a), but also commonly escalating into intense bouts of butting and grappling. These interactions were common and as intense as those observed in some species of *Philanthus* (e.g., Gwynne, 1978; O'Neill, 1983a) and occurred between a territory resident and either an intruder or a male on an adjacent territory. As many as six males were observed simultaneously interacting within a single territory. The head butting interactions, which usually occurred in mid-air, produced a clicking sound audible several meters away. If a conspecific male landed on the ground near a territorial perch, the two often approached head on (sometimes circled one another in the process) and grappled with their mandibles and forelegs, with considerable buzzing. Wrestling males sometimes fell from the perch to the ground (up to 3 meters below) while remaining locked together in combat. These interactions commonly ended with the original resident of the territory leaving and the intruder usurping possession of the perch. In 20 interactions in which we could identify which male was the resident, the intruder usurped possession of the territory seven times (35%). Steiner (1978) reported behaviors similar to those above in the Oregon population.

As in *Philanthus* (O'Neill, 1983a, b) the outcome of aggressive interactions by males in this population was dependent on the relative body sizes of opponents, rather than their status as resident or intruder. In 1982 we captured 120 males, measured their head widths to the nearest 0.1 mm with a pair of VWR Scientific Products dial calipers, gave each individually distinctive markings with dots of colored enamel paint, and released them. This allowed us to monitor the outcome of aggressive interactions with respect to the body sizes of contestants. In twenty interactions in which we knew the body size of both contestants, the winner was larger 14 times, in the same size class 6 times, and never smaller.

Because of the size advantage enjoyed by larger males and the large numbers of males present relative to the number of the territories many males not defending territories were present at any given time. These males had at least two options for obtaining territories. First, they could aggressively usurp a perch from a resident male. Second, they could enter and occupy a territory abandoned by a resident for some reason. This abandonment and replacement was commonly observed and we could artificially induce it by removing a resident from a territory and allowing other males to occupy it. The methods for accomplishing this have been described previously (O'Neill, 1983b). By repeating the removals, we could cause as many as 14 males to occupy a single territory in one day (mean = 3.8 residents; SD = 4.0; range = 1 to 14; N = 10). Of the 48 males removed from territories during these experiments 37 were replaced within 30 minutes by another male; three other times males were replaced, but after intervals of 33 to 72 minutes. The mean time between removal and replacement was only 9.4 minutes (SD = 14.3; range = 1 to 72; N = 40). When the first male ("original resident") removed was replaced, he was usually replaced by a smaller male (seven of eight times; chi-square = 4.5,  $P < 0.05$ ). However, when subsequent residents on the same day were removed, they were replaced by smaller males on 42% of the time (N = 28, chi-square = 0.57, not significant). These results are similar to those obtained on three species of *Philanthus* (O'Neill, 1983a, b).

As also noted by Steiner, males usually persisted at a perch for a short period, often only a few minutes. There were exceptions however. A male marked white-green (the largest marked male in the population) occupied a territory on the morning of 19 July from 1017 until 1129. In one 20 minute interval during which he was observed continuously, he successfully defended his territory 21 times. Another male, marked blue, was present on a territory on 6 July from about 1000 to 1116. However, males were never observed to defend a territory on any given day for the long intervals (i.e., several hours) commonly observed in territorial male *Philanthus* (e.g., O'Neill, 1983a).

Males were seen scent-marking on twigs, sagebrush, grass stems, pine needles, and other plants near their perches, but, without exception, this behavior was extremely brief, rapid, and always in one direction (up) on the stem. While the body was pressed close to the stem, there was no V-shaped posture as described for some species of *Philanthus* (e.g., Alcock, 1975a). Some males (e.g., white-green discussed above) were not observed to scent mark at all, while others did so relatively frequently. One male (blue) scent-marked 4 times in 66 minutes of observation; another (unmarked) scent-marked 16 times in a 20 minute interval. It is noteworthy that *E. flavocincta* is the only species of its genus lacking the transverse bands of close-set hairs on the ventral side of the abdomen (Scullen, 1968). There are, however, abdominal hairs which are fairly dense on the last four sternites.

Two instances of attempted mating were observed in places where territories were aggregated. Steiner (1978) reported observing a copulating pair, presumably in the aggregation of males he was studying. We also captured two females and released them near territorial males. In both cases a swift pursuit resulted.

We spent many hours in an effort to locate nests of females, but after covering much ground, found only one small plot of bare soil 50 m from the territorial area, where three females started nesting on 22 July. One nest was excavated on 2 August; there were five cells at depths of 7 to 11 cm, each provisioned with 3 to 6 weevils,

all of one species, *Orimodema protracta* Horn (Curculionidae). Thus, we obtained the impression that the nests must be widely scattered in this area. Observations in other locations agree with this judgement. An isolated nest found on 7 July 1982 on a path in Hewlett Gulch, several km from Stove Prairie, was also being provisioned with *O. protracta*. Still another, apparently isolated nest was found in Yellowstone National Park, Wyoming, on 12 August 1971; it was being provisioned with the weevil *Trichalophus alternatus* Say. Evans (1970) also reported an isolated nest from Jackson Hole, Wyoming. On the other hand, Scullen (1939) noted "several dozen burrows" extending over "an area as large as the average city block" in Oregon. Also, Bohart and Powell (1956) reported "thousands of burrows" in silt and gravel hills in Sierra County, California. Thus it appears that females do nest in aggregations in some places, but male behavior has not been reported from such sites.

Steiner (1978) noted that there appeared to be no resources for females (i.e., flowers that might serve as nectar sources) within the aggregation of males. This was also true at Stove Prairie, and furthermore, the soil within the territory aggregation was rocky and overgrown with grasses and sage, thus evidently not suitable for nesting.

#### *Eucerceris cressoni* (Schletterer)

As in the preceding species, *E. cressoni* is characteristic of montane regions of the western United States. It is a smaller species and, unlike *E. flavocincta*, it possesses a dense, transverse band of fimbriate hairs on the fifth sternite of the males. This species has commonly been called *fulvipes* Cresson and is so called in the recent *Catalog of Hymenoptera in America North of Mexico* (Krombein et al., 1979). Bohart and Menke (1976) regard *fulvipes* as preoccupied.

Our studies were conducted 22 km west of Livermore, Larimer Co., Colorado, at an altitude of 2,350 m. The species is abundant in late summer, especially on flowers of *Solidago* spp. We found individual males to have established territories at two sites along the sides of a canyon and at one site in a meadow at the floor of the canyon, 11–12 August 1984. These three sites were 200–300 m apart, but there may have been other territories in between that we did not find.

In the sites on the hillside, the males perched on dead, prostrate branches of bushes, surrounded by grasses and sagebrush. In the meadow below, a male had established a perch on a dried cattle dropping surrounded by grass. All three males defended their territories vigorously and scent-marked surrounding vegetation at rapid rate. While perched, they held their antennae rigidly forward and their wings obliquely upward, as described for *E. flavocincta*.

Our more detailed observations were made at the territory closest to the top of the canyon. During a 10-minute period (1036–1046), the resident male scent-marked nearby grass blades 54 times in 41 bouts, sometimes marking 2–5 stems per bout. Between each bout he returned to his perch on dead branches of a bush, less commonly on grass blades. During this period, he interacted four times with a conspecific male, following closely behind in flight and occasionally butting the intruder. During a second 10-minute period (1107–1117) on the following day, the male resident on this territory scent-marked 36 times in 20 bouts and had two interactions with conspecific males. At 1248 on this same day, the resident male was still defending

the territory and scent-marking (21 times), but he left the territory at 1253 for the day.

In all but one of the scent-markings observed, the wasp walked only upward along the stem, not reversing itself as commonly occurs in *Philanthus*. In every case the head and posterior part of the abdomen were pressed against the stem, in a broadly V-shaped posture. From 3–5 cm of the plant were covered in each episode of abdomen dragging.

We made an extensive search for nests in the vicinity of these three territorial sites, but were only able to find one, on 26 August, along a road cut at the top of the canyon, about 150 m from the uppermost territorial site. The nest entrance was beneath a loose rock, in sandy loam. Prey had been stored in the burrow, at depths of 9 and 12 cm, and there were two cells, at depths of 12 and 14 cm, containing 5–7 prey each, with an egg laid longitudinally on top of the prey. All 15 prey were of similar size and form, but consisted of three species, *Otiiorhynchus ovatus* (L.) (11), *Anametis* spp. (3), and *Listronotus obscurus* (Dietz).

Evans (1970) reported finding a group of nests in the midst of an aggregation of *Philanthus crabroniformis* in Jackson Hole, Wyoming, the prey consisting of three species of weevils. Evidently, this species does group its nests in suitable areas of bare soil at times.

#### *Eucerceris superba* Cresson

This large species is characteristic of the Rocky Mountains and western Great Plains, usually in less wooded areas than the preceding two. Males of this species have three transverse bands of fimbriate hairs, on the third, fourth, and fifth abdominal sternites. Both sexes are common visitors to *Eriogonum effusum*. We made brief observations on male behavior at the Great Sand Dunes National Monument, Alamosa Co., Colorado, at an altitude of 2,450 m, 10 August 1983. Two males were seen grappling at 1012 in an area of sparse grasses, cacti, and yuccas on the crest of a small sand hill adjacent to the dunes. The smaller of the two males left the area and the larger maintained a territory in a partially bare area about 1.5 m in diameter. This male perched mainly on the ground, but also on low plants. All scent-markings were on grass blades, and all were upward only, the wasp sometimes covering up to 15 cm on a single marking, assuming a broadly V-shaped posture, with the head and posterior part of the abdomen pressed close to the grass blade.

Over a 10-minute period (1015–1025), this individual scent-marked 27 times in 15 bouts, bouts containing markings on up to four separate grass blades. During this time the male also pursued passing insects.

Scullen (1939) quoted field notes by O. A. Stevens to the effect that males patrol for females and attempt to mate with them on flowers. Stevens also reported a female carrying a weevil, *Ophryastes sulcirostris* Say, in North Dakota. Scullen (1968) later gave a record of a weevil of the same genus taken as prey in Alberta. Evidently nests of this species have never been found.

#### *Cerceris nigrescens* F. Smith

This species is widespread in North America, occurring from coast to coast. The males have fimbriae of short, clumped hairs emanating from sternum VII and ap-



pressed to sternum VIII. Brief observations on this species were made on 28 June 1984, in Hewlett Gulch, 35 km northeast of Fort Collins, Colorado. However, since scent-marking has not previously been reported in this genus, we thought it of value to include the observations in this paper. At 1050 a single territorial male was found on a rabbitbrush (*Chrysothamnus*). The male alternated perching on the plant (15–30 cm off the ground) with flights around the plant, sometimes in pursuit of passing insects. When perched the male adopted the posture described above for *Eucerceris*. The male scent-marked plants, usually the rabbitbrush, walking either up or down the stem, but not assuming a V-shaped posture. During a 15-minute observation period, the male scent-marked 15 times, in bouts of one to three abdomen drags. A search of the area near this territory revealed no other males.

*C. nigrescens* is reported to nest in sandy soil, either as solitary individuals (Peckham and Peckham, 1898), in small aggregations (Evans, 1971), or in groups of as many as 50 females within 10 square feet (Krombein, 1936).

#### DISCUSSION

Population size and nest density of many Cercerini appear to vary greatly. As noted, species of *Eucerceris* and *Cerceris* have been found to have either solitary, scattered nests or to nest in large aggregations. Byers (1978) described great yearly variation in populations of *C. halone* Banks in Virginia. At one site, there were 407 nests in 1967, but only 26 in 1975, and none in 1977. Alcock (1975c) was able to greatly increase the density of nests of *C. intricata graphica* F. Smith (identified as *simplex*) by watering the soil. The unpredictability of nest site occupation by Cercerini stands in contrast to that in *Philanthus*, where populations of several species are known to have been more or less constant at certain sites over many years (e.g., Evans, 1973; O'Neill and Evans, 1983). Since nest distribution is an important factor influencing male mating tactics (Alcock et al., 1978), one might anticipate greater lability in mating systems in Cercerini than in *Philanthus*. Unfortunately, data bearing on this point are fragmentary.

There are many similarities in male territorial behavior of some Cercerini and of *Philanthus*. Males of several species defend territories vigorously with basically similar interactions and scent-mark stems on their territories. It appears that in *Eucerceris* scent-marking males pass only upward along the stem, rather than up and down as in species of *Philanthus* and in *Cerceris nigrescens*. The consistency and significance of this behavioral difference remain to be determined. As in *Philanthus*, there is intense competition for territorial sites and larger males are most successful in maintaining territories. Removal of resident males of *E. flavocincta* usually resulted in occupation of the territory by one of the many non-territorial males present in the area in less than 10 minutes. As in *Philanthus*, rates of scent-marking are lower in the larger species. Many species of *Cerceris* do not appear to exhibit male territoriality or scent-marking. Alcock (1975b) noted that this is the case in *C. frontata* Say and *C. intricata graphica* (identified as *simplex*), two species in which males patrol broad areas for receptive females.

The mating system of *E. flavocincta* appears similar in many respects to that of *Philanthus basilaris* (O'Neill, 1983a). In both species, scent-marking territorial males gather in dense groups to attract receptive females. These "leks" may have evolved

because of the unpredictability of the widely spaced and difficult to locate nests of females, at least in the populations studied by Steiner and us. It will be interesting to see if this mating system prevails in large aggregations such as those studied by Scullen (1939) and Bohart and Powell (1956).

The subfamily Philanthinae appears to be at least as old as 25 million years, since fossils identified as *Philanthus* and *Cerceris* have been discovered in Oligocene deposits. Male territoriality and scent-marking have now been reported in four genera of Philanthinae: *Philanthus*, *Eucerceris*, *Cerceris*, and *Clypeadon* (Alcock, 1975b), including representatives of all three main divisions of the subfamily recognized by Bohart and Menke (1976). Thus, "abdomen dragging" and the associated morphological adaptations (i.e., clypeal and abdominal hair brushes) are probably relatively ancient characters within this group. It seems less plausible that these adaptations have evolved independently as the subfamily has radiated. However, it is evident that there is much evolutionary plasticity in these characters, given the variability in their expression among species. They are most developed in *Philanthus* where most species have highly developed clypeal and abdominal hair brushes and may have extremely high rates of scent-marking. In contrast, some species do not exhibit territoriality and lack well-formed clypeal or abdominal hair brushes. Alcock (1975b) noted that this is the case in *Cerceris frontata* and *C. intricata graphica* (identified as *simplex*). Reduced mandibular glands and the loss of clypeal and abdominal hair brushes in *P. albopilosus* is most likely associated with the fact that, rather than defend territories, males of this species patrol for females in open dune areas (Evans, 1975). It appears that some form of territoriality and scent-marking is ancestral in this group, the behaviors have diversified and, in some cases, secondarily disappeared in the face of the varying selection pressures that mold mating systems.

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## ORIENTATION BEHAVIOR OF THE SLAVE-MAKING ANT *POLYERGUS BREVICEPS* IN AN OAK-WOODLAND HABITAT

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**Abstract.**—The orientation behavior of *Polyergus breviceps* was studied in an oak-juniper woodland in southeastern Arizona. Target colonies of *Formica gnava* were scattered in all compass directions around the *Polyergus* nests. Tests conducted at the front of the slave-raid swarm showed that optical stimuli, especially polarized light, are the principal cues for worker orientation. There was no evidence that the ants were following a chemical trail previously deposited by a successful scout. After the slave raid, workers of *Polyergus* returned to their home nest by responding simultaneously to optical cues and to a chemical trail that they had deposited during the outbound raid. Although it is possible that naive individuals, scouting for the first time, may indeed rely more heavily on a chemical trail, all evidence to date indicates that experienced scouts utilize optical orientation.

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The parasitic formicine ant genus *Polyergus* consists of four species, all characterized by a worker caste that is specialized for conducting group raids on colonies of the related genus *Formica* (Yasuno, 1964; Talbot, 1967; Dobrzńska, 1978; Topoff et al., 1984). Although up to 75% of the raided pupae are eaten (Kwait and Topoff, 1984), those that are reared through eclosion subsequently assume the chores of foraging, brood-rearing and nest maintenance for the mixed-species colony.

Compared with other groups of ants, relatively little is known about the processes of communication and orientation utilized by scouts and raiders during the slave raids. In studies of *Polyergus lucidus*, Talbot (1967) and Marlin (1969) emphasized chemical communication, and concluded that individual scouts deposit a trail from the target *Formica* colony back to their home nest. In a recent study of the western species *P. breviceps* in Arizona (Topoff et al., 1984), we discovered that scouts utilize optical orientation when returning from colonies of *Formica gnava* to their home nest, and when leading nestmates on the slave raid. During the raid, both scout and raiders deposit a chemical trail. After the raid all individuals return by a combination of optical orientation and following the chemical trail deposited on the outbound trip.

The reliance of *P. breviceps* scouts on optical cues in our study may have been enhanced by the unique ecology of our desert study site. All *Formica* nests in this area were located to the south of the experimental *Polyergus* colony, in the narrow riparian zone created by Cave Creek. As a result, practically all scouting and slave

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raiding took place in the same general direction. Under these conditions, experienced scouts may require only optical cues for successful orientation.

In this paper, we report the results of comparable orientation studies, conducted in an oak-juniper habitat where target *Formica* colonies are scattered in all compass directions around *Polyergus* nests. The goal of the study was to determine whether the role of chemical orientation would be increased in this more "complex" habitat.

#### MATERIALS AND METHODS

Studies of orientation were conducted at the Southwestern Research Station of The American Museum of Natural History, located 5 km west of Portal, Arizona. At an altitude of 1,646 m, the dominant vegetation consists of Arizona oak, alligator juniper, and Chihuahuah pine. Two colonies of *P. breviceps* were used for the study, during July and August of 1983.

To elucidate the stimuli utilized by *Polyergus* for orientation during scouting and raiding, a series of tests was performed as the ants moved to (outbound) and from (inbound) target colonies of *Formica gnava*. All studies were conducted between 1600 and 1730 hours (MST), as the ants crossed a predetermined, 2-m wide test area that was relatively devoid of trees. For the inbound test series, observations of the ants' behavior were made after a slave raid, when the number of returning ants crossing the test area was at or near its peak. As indices of the ants' "confusion," we recorded: (1) the number of turns greater than 45° made by test individuals; and (2) the direction in which the ants were oriented (with respect to their home nest) at the end of the test interval. This bearing used 0° as the homeward direction, which was assigned if the ant's posterior-to-anterior axis pointed with a range of 45° to the left or right of the 0° direction. The 90°, 180°, and 270° positions were similarly designated. Each of 15 ants was observed for 30 s, starting when the subject first contacted the test area. For the inbound test series, each of the following conditions was conducted two times:

(a) Control: To provide baseline data for subsequent comparison, two sets of observations were made on returning ants that were not subject to any manipulation.

(b) Diffused sun-normal sky: After the outbound slave-raid swarm had crossed the road, a wooden frame (2.5 m<sup>2</sup>) covered with waxed paper was positioned over the test area at a 45° angle, so that returning ants could not see the sun directly (which was low in the western sky in the afternoon). The frame was positioned with its upper end sufficiently to the west so that the sky directly above the returning ants was fully visible.

(c) Diffused sun and sky: In this test condition the waxed paper frame was suspended horizontally across the test area (1.5 m above the ground), thus diffusing the light from both the sun and the sky overhead.

(d) No trail: After the outbound column had crossed the test area, we used garden hoes to remove the top layer of soil (and therefore any chemical trail that the ants might have deposited on the outbound raid).

A second identical series of tests was conducted on outbound *Polyergus* workers, when the front of the raiding swarm first entered the test area. In this outbound series, the 0° bearing was assigned if the ants' posterior-to-anterior axis pointed away from the home nest.

Table 1. Mean number of turns and chi square ( $\chi^2$ ) distributions for 30 individuals of *Polyergus breviceps* during slave raid (outbound) and return (inbound) trip.

Test condition	Inbound			Outbound		
	Mean no. turns	$\chi^2$	P	Mean no. turns	$\chi^2$	P
Control	0.9	30.6	<0.01	1.4	18.7	<0.01
Diffused sun-normal sky	1.1	30.5	<0.01	1.9	24.7	<0.01
Diffused sun and sky	9.3	0.7	NS	10.6	1.3	NS
No trail	8.0	1.3	NS	1.2	24.7	<0.01

NS = not significant.

### RESULTS

The orientation behavior of *Polyergus* in the two test series is represented in Table 1. All values in the table were calculated by combining the data for the two replicates of each test condition. Comparisons of turns were based upon an analysis of variance. Because the analysis showed a significant effect for conditions [ $F(7,112) = 53.3$ , and  $P < 0.01$ ], we utilized a Tukey test of multiple comparisons to determine significant differences among condition means (with  $P < 0.01$ ). A chi square test was utilized to indicate whether the number of ants moving toward each of the four compass directions represented a random distribution.

In the unmanipulated control condition (inbound series), the mean number of turns was 0.9 and 87% of the returning ants were moving in the homeward direction at the end of the observation period. This clearly represents a non-random distribution with respect to the four possible directions ( $\chi^2 = 30.6$  in Table 1). When the ants could only see a diffused sun, but a normal sky directly overhead, their orientation behavior was essentially unchanged. However, when the waxed-paper frame was placed horizontally over the returning ants (so that the light from both the sun and sky were diffused), the efficiency of their homing behavior decreased markedly. The mean number of turns was significantly greater than that of the control and "diffused sun-normal sky" conditions, and the chi square test showed that the ants were moving randomly. Finally, removal of the chemical trail, even though the ants' view of the sun and sky was not obstructed, had an equally disorienting affect on their homing behavior. The mean number of turns, although significantly greater than that of the control and the "diffused sun-normal sky" conditions, was not significantly different from that of the "diffused sun and sky" condition.

In the outbound test series, conducted when the slave raiders were en route to the target *Formica* colony, the first condition again served as a control. Our observations began when the front of the raid swarm entered the test area. In the control condition, the mean number of turns made by the 30 observed raiders was 1.4, and the ants were oriented toward the target nest ( $\chi^2 = 18.7$ ). In the "diffused sun-normal sky" condition, the orientation of the advancing slave raiders was again correct. In the "diffused sun and sky" condition, however, the advancing raid came to an abrupt halt as soon as the ant swarm entered the area of testing that was covered by the waxed-paper frame. The mean number of turns was significantly greater than that

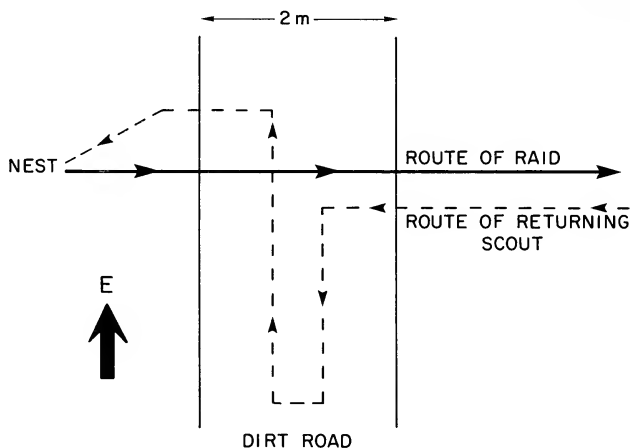


Fig. 1. Path of returning scout (broken line) whose route was artificially altered, compared with route of slave raid (solid line) subsequently led by the same scout.

of the first two test conditions, and the ants were moving randomly over the four compass directions ( $\chi^2 = 1.3$ ). When the haphazard movements of the *Polyergus* brought them beyond the boundaries of the waxed-paper frame, they immediately resumed their forward direction. In the last experimental condition, when the advancing ants crossed the test area that had its top layer of soil removed prior to raid onset, the ants' behavior was not significantly different from that of the control.

An additional manipulation further demonstrated the ants' reliance on optical cues. It was conducted during a slave raid towards a colony of *Formica* located 40 m to the south. Prior to raid onset, an outbound scout was marked (on its gaster) with fluorescent powder. When it returned to its home nest, we used a 1.5-m long sheet of plywood to divert its path (Fig. 1). The scout was forced to change direction twice (2 m to the west, followed by 3 m to the east) before resuming its homeward (north) route. Despite this displacement, the scout promptly led a successful slave raid along a straight course to the south.

#### DISCUSSION

The results of this study of in the oak-juniper woodland are consistent with those from our previous research in the desert habitat (Topoff et al., in press). Thus, although colonies of *Formica gnava* were scattered in all compass directions, the tests in the outbound series showed that *Polyergus* orientation at the raiding front is not based upon chemical cues. Although we did not mark individual ants, our previous study with marked scouts (Topoff et al., in press) showed that most raids are indeed initiated and led by a single scout. In addition, although we have not analyzed the ants' ability to utilize visual landmarks or canopy outlines (Hölldobler, 1980), their severe disorientation under the waxed-paper (which diffuses light) suggests that polarized light may be the principal stimulus (Wehner, 1969). Our previous desert study also showed

that the position of the sun is an additional cue, because *Polyergus* workers could be reversed by "displacing" the sun's direction with a mirror.

Results from the inbound test series indicate that workers of *Polyergus* returning from a raid orient by responding simultaneously to optical cues and to a chemical trail that they deposited on the outbound slave raid. Such simultaneous reliance on diverse sensory processes is well documented for many ants, including the genera *Neivamyrmex* (Topoff and Lawson, 1979; Topoff et al., 1980) and *Pogonomyrmex* (Hölldobler, 1976)

Perhaps the most obvious discrepancy between our findings and those from studies of the eastern species *P. lucidus* (e.g., Talbot, 1967; Marlin, 1969) is our conclusion that *P. breviceps* scouts rely on optical rather than chemical stimuli for orientation. It is of course possible that *Polyergus lucidus* and *P. breviceps* scouts utilize different cues. A more likely explanation for the discrepancy, however, is that studies of *P. lucidus* have only demonstrated orientation over artificially-deposited chemical trails. In none of these studies was the role of optical orientation even considered. We favor the optical orientation hypothesis because it is consistent with the method by which *Polyergus* slave-raid swarms typically find target nests of *Formica*. In studies conducted with marked ants (Kwait and Topoff, in press; Topoff et al., in press) it was observed that the original scout is frequently *not* the individual that relocates the target colony. The scout runs intermittently at the head of the raid swarm, and usually leads the raiders only to the general area of the *Formica* nest. She then stops advancing (and presumably also stops depositing the recruitment trail). When this occurs, the *Polyergus* workers (which may number more than 2,000 individuals) also cease advancing, and fan out over a roughly circular area up to 3 m in diameter. Because any *Polyergus* worker that encounters the *Formica* colony can recruit nestmates, the scout need not relocate the target nest with pinpoint accuracy. The adaptive value of utilizing optical cues rather than a chemical trail can be appreciated by considering that target *Formica* nests may be located up to 100 m from the *Polyergus* colony, and that a scout may require more than 1 hr to make the round trip. As a result, a chemical trail deposited by a single scout over such a long distance could easily be disrupted by rain, wind-swept leaf litter, or animal traffic.

Despite the findings from our studies of *Polyergus* orientation, there is one condition in which it might be more adaptive for scouts to rely on a chemical trail. We have previously determined for *P. lucidus* (Kwait and Topoff, in press) that workers do not become scouts until the second season after their eclosion. In the pattern of temporal polyethism that exists for *Polyergus*, workers progress from inside-the-nest activities to preraid circling to scouting. It is thus quite possible that individuals scouting for the first time may deposit a chemical trail from the target *Formica* colony back to their home nest. As they become more experienced, optical cues may then replace the chemical trail. This would be similar to the temporal change in orientation cues described by Henquell and Abdi (1981) for *Formica polyctena*. In conclusion, as Hölldobler (1980) correctly noted, many social insects have a hierarchy of available cues for orientation (and undoubtedly also for communication). Which cues are utilized, and in what combinations, depends upon many factors, including the species' sensory capabilities, social context, stimulus availability, and the age and experience of the individuals.



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## COOPERATIVE COLONY FOUNDATION BY FEMALES OF THE LEAFCUTTING ANT *ATTA TEXANA* IN THE LABORATORY

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**Abstract.**—We describe a simple procedure for rearing colonies of the Texas leafcutting ant, *Atta texana* (Buckley), from foundress females in the laboratory. The progress and outcome of cooperative colony foundation attempts by several females is described. The results show that cooperative colony foundation (pleometrosis) in *A. texana* can lead to large polygynous colonies.

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The leafcutting ants of the genus *Atta* have a major impact on natural and agricultural plant communities in the New World tropics and warm temperate zone. Available data suggest that most *Atta* species have monogynous colonies, but polygyny is commonly encountered in the Texas leafcutting ant, *Atta texana* (Buckley) (Moser, 1981). Colony founding females may aggregate and cooperate in excavating a common burrow after the mating flight. Multiple inseminated dealate females have been removed from established colonies in the field (Moser, 1967; Echols, 1966). Echols showed that young colonies could be joined together without aggression to produce artificially polygynous colonies in the laboratory.

Although colony foundation by some *Atta* species in the laboratory has been described (Huber, 1905; Autuori, 1956; Weber, 1972), the outcome of colony foundation attempts by cooperating females (pleometrosis) has not been previously examined in *A. texana*. Cooperative colony foundation in ants very rarely leads directly to mature polygynous colonies (Hölldobler and Wilson, 1977). Usually, extra foundress females are eliminated early in the colony life cycle, often before the first workers eclose. Most mature polygynous ant colonies apparently originate through the secondary adoption of additional inseminated females. Although Moser (1981) asserts that "*Atta texana* is the only known occurrence of pleometrosis leading smoothly to polygyny in ants," he does not provide any colony life histories to support the claim. This report describes simple techniques for the establishment of *A. texana* colonies in the laboratory, which were used to follow the progress of cooperating foundress females.

### MATERIALS AND METHODS

Dealate females of *A. texana* were collected as they excavated burrows after mating flights in May 1983 and 1984. The flights occur before dawn on days after rainfall. Females were collected between 1000 and 1200 hours local time at three sites. In 1983, 13 females were collected at a greenhouse on the Texas A&M University campus and along a highway 22 km south of the campus. In 1984, 30 females were

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collected at Washington-on-the-Brazos State Park. The latter two sites were less than 100 m away from mature *A. texana* colonies, but the first site was probably at least 1 km from the nearest colony. None of the collection sites were near artificial lights, which attract alates (Moser, 1967). At each site, dealate females were concentrated in relatively small areas on barren or scattered grass and weed covered soil, and some females were found together, excavating a common burrow. One such group of five dealate females (Fig. 1) was kept together after collection in 1984. The others were reassembled in groups of two or three females for study of colony foundation in the laboratory.

The ants were placed in 10 × 7 cm high clear plastic dishes, lined along the bottom with perlite granules premoistened with distilled water. The closed dishes were kept in an incubator at approx. 27°C and 65% RH with a 16 hr day/8 hr night photoperiod, and were not reopened until worker eclosure was imminent. However, dying females were removed promptly and the spermatheca was examined upon dissection. In 1984, ten females were individually weighed and marked and grouped into five pairs.

When workers were expected, the dish lid was removed and fitted with a vertical plastic tube, initially plugged with a cork. The dish and tube were placed in or connected to a larger plastic foraging arena. Young colonies were maintained on a diet of cornmeal and oatmeal.

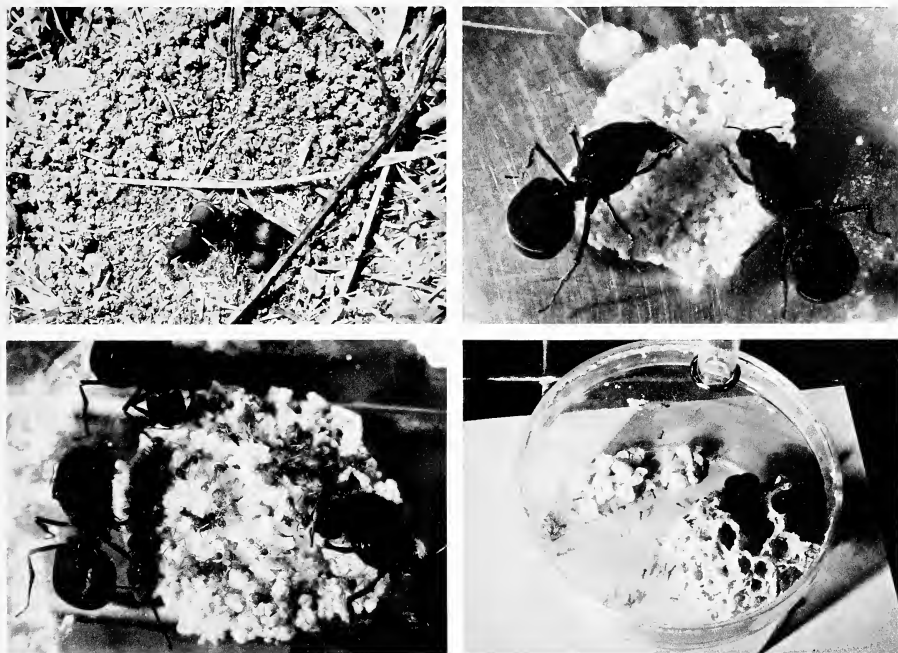
#### RESULTS AND OBSERVATIONS

The females regurgitated infrabuccal pellets within 24 hr after placement in the dishes and began oviposition after 24–48 hr. The females removed the perlite from an area in the center or on one side of the dish and kept their brood and fungus on the plastic surface in this cleared zone. They cultured the fungus and droplets of fecal fluid, as described for many other attine ants (Autuori, 1956; Wheeler, 1907; Weber, 1972). The fungal mat grew into a disk 20–30 mm across within four weeks (Fig. 2) and then remained about the same size until workers added new substrate later on.

Each female contributed eggs during pleometrotic colony foundation. The egg stage lasted 14–16 days. The females fed larvae with freshly laid eggs. Again, each female participated in larval feeding. Pupae appeared in the first brood eight to 10 days after the eggs hatched, and required 14 more days to complete development. In 1983, two groups of females required 40 days to rear workers in the laboratory. Each of five groups of females required 36 days to rear workers in 1984. Moser (1967) concluded that females of *A. texana* require 40–50 days to rear workers to maturity in the field in Louisiana. Not all groups survived to rear workers; two of four groups set up in 1983 lost their fungus to bacterial contamination and died with larval brood.

Females were placed together without any difficulty. In one case, dealate females collected at different sites were paired and successfully started a colony (Figs. 2, 4). Oral trophallaxis between females was not common, and allogrooming was not observed except when females were initially grouped. As a possible consequence, some females developed growths of opportunistic filamentous fungi on the dorsal surfaces of the gaster and thorax. The fungal growths did not seem to harm the females, but they were quickly removed by the first workers.

After flight, the mean weight of dealate females was 387 mg (N = 10; range: 349–423 mg). One of five pairs of weighed females failed to rear workers, but both females



Figs. 1–4. 1 (upper left). Cooperative burrow excavation by five *A. texana* females. The gasters of two digging females are visible, while a third female carries a soil pellet away from the entrance. 2 (upper right). A pair of females with their fungus after three weeks. Eggs and larvae are visible in the center of the fungal mat. 3 (lower left). Successful colony foundation by three cooperating females. Fungus, brood, and young workers are visible. One worker is grooming the gaster of the female at left. This colony died nine months later; spermathecal examination showed that all females had mated. 4 (lower right). Successful colony foundation by two females in Fig. 2. Two months after the first worker eclosed, the ants have removed all but the largest perlite granules through the exit tube at top center.

were inseminated. An inseminated female in a second pair died after 13 days. She had lost 22 mg and was replaced with another weighed ant. The replacement female had lost 122 mg when the first workers eclosed. The other seven females had lost 71–143 mg (mean 118 mg) when the first workers appeared, or about 30% of initial body weight (range: 20–36%).

Most first brood workers were three to four mm long, as Moser (1967) found in field samples, although a few smaller workers were also present. The first workers began to groom other individuals and tend brood within three days (Fig. 3). They also began exploring the dish interior and were walking on the sides and inner lid surface within five to seven days. Six to eight days after eclosure, the workers discovered the exit tubes and foraging began when the cork was removed. Ten days after the first worker eclosed, each pair of females had approximately 45–55 workers, while the group of five females had about 36 workers. Eight to 10 days after eclosure, the workers began to shape the material on the outer margin of the fungal disk into



ridges, producing a miniature 'amphitheater' with brood piled in the center as new substrate was added to the ridges. The workers removed the perlite from the culture dish and dumped it within two months as the fungus grew to about 50 ml (Fig. 4). One pair produced their first major worker in October 1983, five months after the females were collected.

#### DISCUSSION

Although this report and previous studies by Moser (1967, 1981) and Echols (1966) show that pleometrotic colony foundation attempts are common in *A. texana* and can lead directly to large polygynous colonies, the advantages of cooperative colony foundation remain less obvious. High genetic relatedness between females is not a prerequisite for pleometrotic colony foundation. Waloff (1957) suggested that co-operating ant females benefit from mutual grooming to remove pathogenic micro-organisms. Such behavior would seem particularly advantageous to ants like *A. texana* which must also maintain an uncontaminated fungus culture. Our failure to observe allogrooming is surprising, since the females carefully lick the plastic surfaces near the brood and fungus, and continue their routine self-grooming behavior.

Mated females which lack viable infrabuccal fungus pellets will obviously benefit by joining groups with viable fungus. Weber (1972) found that colony founding females of some *Atta* species commonly lacked fungal pellets after the mating flight. However, a careful count of regurgitated pellets showed that nearly all of our *A. texana* females contributed pellets after installation in culture dishes. Nevertheless, different pellets might still vary greatly in viability.

Cooperation during digging may allow females to complete and seal the natal burrow more quickly. Females which remain on the surface were quickly located and attacked by *Solenopsis invicta* (Buren). Although high *Solenopsis* population levels are only a recent problem, other opportunistic ant predators such as *Pheidole* spp. and *Iridomyrmex pruinosum* may have been a long term threat to *A. texana* females on the ground. In western Mexico, colony founding females of *A. mexicana* (F. Smith) were attacked by *Pheidole* spp., *Iridomyrmex pruinosum* (Roger), and the native *Solenopsis xyloni* McCook (Mintzer, pers. obs.). However, *A. mexicana* females did not excavate cooperative burrows and were aggressive when placed together. A comparative field study of colony foundation in the two *Atta* species might illuminate the factor(s) responsible for pleometrosis and polygyny in *A. texana*.

#### ACKNOWLEDGMENTS

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## GENERAL ACTIVITY AND REPRODUCTIVE BEHAVIOR OF *RHAGOLETIS CORNIVORA* (DIPTERA: TEPHRITIDAE) FLIES IN NATURE

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**Abstract.**—Data from field observations on the location and activity of *Rhagoletis cornivora* Bush flies on *Cornus amomum* Mill. revealed the following. Females made more visits to each of fruit, leaves, and branches than did males. Females fed while on the upper surface of leaves and much more often than did males. While females spent almost as much time on leaves as they did on fruit searching for suitable oviposition sites, males spent most of their time on fruit clusters, either searching or waiting for potential mates. Most encounters between flies occurred on fruit. Males mounted other males as often as they did females, indicating the inability of males to distinguish between the sexes. Unripe fruit were preferred over ripe ones for oviposition.

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The family Tephritidae (Insecta: Diptera) comprises many species of flies whose larvae feed in the flesh of growing fruits or vegetative tissues and often constitute major agricultural pests. Members of the genus *Rhagoletis* infest a broad range of fruits, including cherry and walnut. The four members of the *pomonella* species group are so morphologically similar that originally they were considered to be "host races," or biotypes, of a single species (Pickett, 1937), each feeding solely on plants in a different family: *R. pomonella* (Walsh) on apple, hawthorn, plum, cherry, and rose hips (Rosaceae); *R. mendax* Curran on blueberry (Ericaceae); *R. zephyria* Snow on snowberry (Caprifoliaceae); and *R. cornivora* on dogwood (Cornaceae). Ecological (see Bush, 1966; Boller and Prokopy, 1976, and references therein) and biochemical (Simon, 1969; Berlocher, 1980; Berlocher and Bush, 1982) studies have shown these four flies to be distinct species. Although the natural history and behavior of the economically-important *R. pomonella* (Prokopy et al., 1972; Dean and Chapman, 1973; Reissig and Smith, 1978; Smith and Prokopy, 1980) and *R. mendax* (Lathrop and Nickels, 1932; Smith and Prokopy, 1981, 1982) flies have been well studied, little is known about the other two species. Here, I present the results of observations of *R. cornivora* adult activity in nature.

### MATERIALS AND METHODS

This study was conducted during the summer of 1981 in Champaign, Illinois. *R. cornivora* behavior was observed on a group of five heavily-fruited silky dogwood bushes that reached 2 m in height. Data were collected between 0900 and 1300 hours CST on each sunny or partly sunny day from 7 to 12 August, beginning four days after the first fly sighting.

Flies were selected randomly by blindly pointing at a branch and watching the fly closest to the selected spot. Flies were watched for as long as they remained in view, up to a maximum of five minutes. I watched each fly from ca. 30 cm away. As long

Table 1. *R. cornivora* visits and time<sup>a,b</sup> spent on silky dogwood plant parts by 41 males and 62 females.

Sex	Location	No. of visits	Total time	Mean time/visit	Mean total time/fly
Male	Fruit	96	7,112	74a	173a
	Leaves	53	997	19b	24b
	Branches	7	22	3c	1c
Female	Fruit	425	5,840	14b	94d
	Leaves	266	4,820	18b	78d
	Branches	21	106	5c	2c

<sup>a</sup> In seconds; maximum 300 sec per fly.

<sup>b</sup> Any 2 means in each column followed by the same letter are not significantly different at the 5% level using Student *t*-test.

as I avoided sudden movement, my presence did not appear to affect fly behavior. Fly activities were recorded verbally on tape and later transcribed for analysis.

Fly activities were defined as follows: feeding was lowering the proboscis to touch the surface on which the fly was situated; an encounter was a meeting of two flies in which there appeared to be recognition by each fly of the other's presence; mounting was a male attempting copulation with another fly by flying or leaping onto its abdomen; boring was insertion of the ovipositor into a fruit; and oviposition was deposition of an egg as evidenced by subsequent ovipositor dragging (Prokopy et al., 1976).

On 10 August, 80 fruit clusters were randomly chosen, in the same manner as the flies, and inspected on the bush to determine the relative numbers of fruit available to the flies for each of three categories of maturity, as judged by skin color. *C. amomum* fruit changed from green to green-blue to blue.

Statements of comparison are supported by chi-square or Student's *t*-test.

## RESULTS

The activities of 41 males and 62 females were observed. Table 1 gives the number and duration of visits to plant parts by each sex. Males moved among plant parts less often than did females. Most male time was spent on fruit, as reflected both by the larger number of visits ( $\chi^2 = 11.8$ ,  $P < 0.005$ ) to and by the greater time spent per visit ( $t = 5.68$ ,  $P < 0.001$ ) on fruit compared with leaves. Females also made more visits ( $\chi^2 = 36.13$ ,  $P < 0.005$ ) to and spent more total time ( $\chi^2 = 97.4$ ,  $P < 0.005$ ) on fruit than on leaves. Neither sex spent much time on branches. Nine males, but no females, spent the full five minute observation period on an individual fruit. No fly remained this long on a leaf. Although females visited more fruit than did males, males spent more time there since the mean length of visit was much greater ( $t = 6.51$ ,  $P < 0.001$ ) than for females. Females spent more time on leaves than did males ( $t = 3.28$ ,  $P < 0.005$ ). The mean observation periods for males and females were 198 sec (SD 108) and 174 sec (SD 110), respectively.

All feeding occurred while on the upper surface of leaves, where flies found substances resembling insect honeydew in one male and 25 female visits.

A total of nine male-female encounters was observed. Both encounters on leaves began with the flies facing one another and led to a short flight or leap by the male onto the female, resulting in mating. In all encounters on fruit, the female apparently was searching the fruit for a suitable oviposition site. Five of the seven encounters there led to mounting and two of these resulted in mating, both of which began with a male making a rear approach to a female while she was boring into the fruit. The male approached the female from the front in the two encounters that did not lead to mounting. The male approached from the rear or side in the three mounts that did not lead to mating. Whether on a leaf or fruit, no female approached a male. Whenever mounting did not occur, it was the female who left first. During those mounts that did not result in mating, the female repeatedly lifted her wings and sharply turned her body in an apparent effort to dislodge the male. This female resistance did not occur during mounts which led to mating.

One encounter between females occurred on a fruit and both flew away. Male-male encounters were mostly on fruit. Mounting occurred after four of five encounters on fruit and after the one on a leaf. The two males were head-to-head before all of these mounts. There was no apparent recognition by the mounting fly that the mounted one was another male, especially since two males were dislodged, by movements similar to those of resisting females, and then tried to remount.

Only 5.2% of female visits to fruit led to oviposition. Boring without egg deposition occurred in 1.4% of visits. Before boring, a female usually walked around the fruit for several seconds, apparently searching for a suitable oviposition site. Upon finding one, she held her upraised body with the tip of the abdomen nearly touching the surface, extended the ovipositor to it and pumped the abdomen up and down several times until the fruit skin was punctured. Oviposition took a half to several minutes. Almost immediately afterward, she walked rapidly around the fruit several times while dragging the extended ovipositor on the fruit surface. When finished dragging, she cleaned the ovipositor for several seconds with the metathoracic legs and then left the fruit. Often this cleaning continued at another site. Although some females bored more than once per visit, they did not oviposit more than once. Females preferred green fruit to riper fruit for oviposition ( $\chi^2 = 7.68$ ,  $P < 0.01$ ). They deposited an egg in 18 of 24 green, 3 of 3 green-blue, and the 1 blue fruit into which they bored. The percentages of these fruit types on the bushes were 55, 23, and 22, respectively.

#### DISCUSSION

The general activity pattern of *R. cornivora* flies was similar to that of *R. mendax* (Smith and Prokopy, 1981) and *R. cingulata* (Smith, 1984). Females search for food and oviposition sites while males wait on fruit for approaching females. As in some other *Rhagoletis* species (Prokopy, 1976; Webster et al., 1979; Smith and Prokopy, 1981), *R. cornivora* females fed more often than males. They are larger than males (Middlekauff, 1941) and presumably need more energy to sustain greater activity and biomass and more protein to produce mature eggs. However, it is unclear why males appeared to feed so seldom. Perhaps, as in *R. mendax* (Smith and Prokopy, 1981), most male feeding occurred early or late in the day and therefore was not observed in this study. Also, *R. mendax* (Smith and Prokopy, 1981) and *R. cingulata* (Smith, 1984) males fed most often on the juice of damaged fruit. Damaged dogwood



fruit were scarce, thus depriving *R. cornivora* males of a ready food source while they were perched on fruit and watching for foraging females.

The mating behavior of *Rhagoletis* flies seems to follow a common pattern. Females are receptive to mating while on leaves, usually when ovarially-immature and not yet ovipositing, but not while on fruit, where they often are force-mated while engaged in some form of oviposition behavior and unable to resist a mounting male, especially when the ovipositor is exposed. This appears true for *R. pomonella* (Smith and Prokopy, 1980), *R. mendax* (Smith and Prokopy, 1982), *R. cingulata* (Smith, 1984), and now for *R. cornivora*.

In common with *R. cingulata* (Smith, 1984), *R. cornivora* females chose unripe over ripe fruit for oviposition. This preference may be advantageous if fully mature fruit do not fulfill the nutritional requirements of the larvae or if ripe fruit are more likely than unripe ones to drop to the ground and then rot or desiccate before the larvae are fully developed.

#### ACKNOWLEDGMENT

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**DICTYLA ECHII: SEASONAL HISTORY AND NORTH AMERICAN  
RECORDS OF AN IMMIGRANT LACE BUG  
(HEMIPTERA: TINGIDAE)**

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*Abstract.* — *Dictyla echii* (Schrank), a Palearctic lace bug associated with boraginaceous plants, has been recorded previously in North America from Maryland, Pennsylvania, Virginia, and West Virginia; additional records are cited for these states, and new records are given for New York and Ohio and for Ontario, Canada. The seasonal history and habits of *D. echii* on viper's bugloss or blueweed, *Echium vulgare* L., in southcentral Pennsylvania are presented. A diagnosis of the adult and a summary of its habits in the Old World are provided.

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The lace bug *Dictyla echii* (Schrank), placed in the genus *Monanthia* LePeletier & Serville until Drake and Ruhoff (1960) resurrected *Dictyla* Stål, is indigenous throughout much of the Palearctic Region. It ranges from Portugal and Spain north to Scandinavia and Siberia, and south to northern Africa, Iran, Turkestan, and China; it is absent from Great Britain (Drake and Ruhoff, 1965; Jing, 1981). This specialist on plants of the Boraginaceae is especially common on species of *Anchusa*, *Cynoglossum*, *Echium*, *Pulmonaria*, and *Symphytum* (Gulde, 1938; Stichel, 1960); Drake and Ruhoff (1965) give a list of known European hosts.

Adults overwinter in the soil near rosettes of *Echium vulgare* L., one of its preferred hosts (Vayssieres, 1983), or occasionally in empty galls made by the phylloxeran *Tetraneura ulmi* (L.) (Stichel, 1960). In spring, eggs are deposited in stems, petioles, and principal veins of host foliage (Štusák, 1958; Vayssieres, 1983). Adults and nymphs feed on rosettes and flower shoots, causing a chlorotic appearance of foliage, stunted floral shoots and, in heavy infestations, a decrease in seed production. Several generations are produced annually (Vayssieres, 1983). Štusák (1958) and Puchkov (1974) described the egg with the latter work containing an illustration, Stusak (1957) and Cobben (1958) described and figured the fifth-instar nymph, and Puchkov (1974) and Vayssieres (1983) provided an illustration of the fifth instar and the adult.

The first records of this lace bug's establishment in the Western Hemisphere were based on specimens collected in 1959 at several localities near Harrisburg, Pennsylvania (Udine, 1962). Hambleton (1968) gave the first records of *D. echii* from Maryland, Virginia, and West Virginia and noted that it had been taken at Miami, Florida, in 1944. Because this latter record was not stated to represent a port interception, Slater and Baranowski (1978) cited Florida as part of the known North American range. The Miami record, however, was based on a live specimen collected in an airplane that had arrived from a foreign country (Drake Collection in U.S. National Museum of Natural History).

Hambleton (1968) also reported that *D. echii* occurs on *Echium vulgare*, a naturalized European plant known as viper's bugloss or blueweed. This biennial weed often colonizes disturbed sites such as road embankments, railroad right-of-ways, and overgrazed pastures, especially in limestone regions (Pusateri and Blackwell, 1979). Two other recent immigrants from the Old World are associated with *E. vulgare*: the megachilid bee *Hoplitis anthocopoides* (Schenck) (Eickwort, 1971, 1973) and the gelechioid moth *Ethmia bipunctella* (F.) (Oecophoridae) (Heppner and Powell, 1974). Eickwort noted that the arrival of an oligotrophic bee of *E. vulgare* provided an excellent opportunity to follow the spread of an exotic insect under nonagricultural conditions. Here, we document the range expansion of *D. echii* on *E. vulgare* in eastern North America, giving New York and Ohio as new state records, listing additional localities for Maryland, Pennsylvania, Virginia, and West Virginia, and providing the first Canadian records (Ontario). We also give information on its seasonal history and habits and provide a diagnosis and an illustration of the adult.

#### MATERIALS AND METHODS

As part of survey and detection work on immigrant insects in eastern North America (Hoebeke and Wheeler, 1983), we checked numerous stands of *E. vulgare* for the presence of *D. echii*. Voucher material from our surveys is housed in the insect collections of Cornell University and the Pennsylvania Department of Agriculture. Records from Albany Co., New York from G. C. Eickwort's study of *Hoplitis anthocopoides* were obtained from undetermined specimens in the Cornell collection.

Seasonal history of *D. echii* was followed by sampling a roadside colony of *E. vulgare* near Harrisburg, Pennsylvania. The plants were growing at the base of a slope planted with crownvetch (*Coronilla varia* L.) that was not mowed. Collections and observations were made every 6–8 days from 27 April to 5 August 1981 and then periodically until plants dried up (usually mid- to late August). Early-season observations were made in May and June 1982. On each sample date, plant material was collected and examined in the laboratory for eggs, and all stages of *D. echii* present were recorded; when nymphs were found, a random sample of 10 was collected and sorted to stage in the laboratory. Nymphs of all stages often occurred on the plants, sometimes in aggregations of a particular instar. Therefore, additional observations were made to determine the presence of nymphal stages that might not be represented in the sample of 10. Nearby colonies of *E. vulgare* exhibited somewhat different phenologies, especially when regular mowing prolonged the normal flowering period. Collections and observations were made periodically from several of these colonies during 1981 and 1982.

#### NORTH AMERICAN DISTRIBUTION

In addition to the published records of *D. echii* from Pennsylvania (Dauphin Co.) (Udine, 1962) and Maryland (Frederick and Montgomery Co.), Virginia (Clarke and Loudoun Co.), and West Virginia (Jefferson Co.) (Hambleton, 1968), the following records are available. Unless noted otherwise, all records are based on the authors' collections from *Echium vulgare*; note the collection from *Cynoglossum officinale* L. in Erie Co., New York.

UNITED STATES. **Maryland:** *Garrett Co.*, Rt. 48, 3 mi E of Grantsville, 25 June 1981. *Washington Co.*, Rt. 63 nr. Williamsport, 14 Aug. 1982. **New York:** *Albany Co.*, Rensselaerville, 17 July 1969, G. & K. Eickwort coll.; 4 June 1970 and 29–30 June 1975, G. C. Eickwort coll. *Broome Co.*, Binghamton, 23 July 1983. *Cayuga Co.*, Auburn, 26 June 1982. *Chemung Co.*, Elmira, 18 July 1981. *Cortland Co.*, Cortland, 11 July 1981. *Erie Co.*, Tonawanda, 31 Aug. 1980; 14 June 1981, on *Cynoglossum officinale*. *Madison Co.*, Rt. 20, 1.3 mi W of Oneida Co. line, 30 June 1984. *Onondaga Co.*, Solvay, 26 June 1982 and 14 May 1983. *Wayne Co.*, Lyons, 31 July 1981. **Ohio:** *Stark Co.*, Louisville, 4 July 1982, K. Valley coll. **Pennsylvania:** *Bedford Co.*, nr. Schellsburg, 2 July 1980. *Berks Co.*, Rt. 78, 1 mi W of Rt. 737 nr. Kutztown, 14 July 1981. *Blair Co.*, Rt. 22 at junc. Rt. 866 nr. Williamsburg, 17 July 1973 and 14 May 1981. *Centre Co.*, State College, 23 July 1980 and 26 Aug. 1981. *Clearfield Co.*, Clearfield and Philipsburg, 26 Aug. 1981. *Cumberland Co.*, nr. Newville, 16 May 1972, T. J. Henry coll.; Rt. 11 nr. Carlisle, 17 Apr. 1974, on *Pinus virginiana*; Rt. 641, 2 mi E of Newburg, 5 May 1973, on *Pinus virginiana*; PA Turnpike, 9 mi W of Rt. 997, 2 July 1980; Enola railroad yards, 10 Aug. 1980 and 5, 27 May 1981. *Dauphin Co.*, Rt. 22-322, NW of Harrisburg, May–Aug. 1981 and May–June 1982; Harrisburg (several sites), May–June 1980–1982. *Fayette Co.*, Conneville, 18 Aug. 1982. *Fulton Co.*, PA Turnpike, nr. Ft. Littleton, 25 June 1981. *Huntingdon Co.*, Greenwood Furnace, 21 July 1982, K. Valley coll. *Lancaster Co.*, Columbia, 22 July 1981. *Luzerne Co.*, Ashley and nr. Mountain Top, 4 Aug. 1983. *Northumberland Co.*, Watsonstown, 7 July 1982. *Somerset Co.*, E of Fairhope, 25 June 1981. *Susquehanna Co.*, Susquehanna, 30 July 1981. *Westmoreland Co.*, New Stanton, 18 Aug. 1982. *York Co.*, Rt. 15 nr. Dillsburg, 15 June 1980; Rt. 30 E of York, 22 July 1981. **Virginia:** *Augusta Co.*, I81N, Rest Area S of Weyers Cave exit, 5 July 1982. *Bath Co.*, SW of Millboro, 10 June 1984. *Carroll Co.*, I77N, 20 mi N of No. Car. state line, 5 July 1981. *Frederick Co.*, Winchester, 25 May 1981, G. C. Eickwort coll. *Highland Co.*, Rt. 678, S of McDowell, 10 June and 15 July 1984. *Rockbridge Co.*, I81S, 5 mi N of Lexington, 3 July 1980. *Smythe Co.*, I81S, nr. Marion, 15 July 1982. *Wythe Co.*, I77N, N of Carroll Co. line, 6 July 1980. **West Virginia:** *Berkeley Co.*, Rt. 11 N of Martinsburg, 2 July 1980 and 14 Aug. 1982; Inwood, 2 July 1982. *Greenbrier Co.*, 6 mi W of Lewisburg, 19 July 1978. *Hampshire Co.*, Rt. 50, 4 mi E of Romney, 14 Aug. 1982. *Hardy Co.*, Rt. 55, Baker, 9 June 1984. *Jefferson Co.*, Shepherdstown, 1 June 1980. *Pendleton Co.*, Rt. 220, S of Franklin, 9 June 1984; nr. Upper Tract, 14 July 1984.

CANADA. **Ontario:** *Grey Co.*, Mt. Forest and Owen Sound, 15 July 1983.

#### SEASONAL HISTORY AND HABITS

Although most adults of *D. echii* may overwinter in soil near rosettes of *E. vulgare* (Vayssieres, 1983), we collected adults, perhaps overwintering individuals, from Virginia pine (*Pinus virginiana* Mill.) during mid-April and early May. At the main sample area in 1981, adults appeared on *E. vulgare* foliage between 27 April and 5 May. Most occurred on lower leaf surfaces, but one mating pair was observed on the upper surface. By 15 May adults were more numerous; mating pairs and eggs were observed. A few eggs were placed in soft tissues of the upper or lower leaf surface, but most were inserted in midribs of the lower surface. As noted by Vayssieres, the



dark brown or black eggs are covered by a conelike, dark gummy substance. Opercula were either flush with the surface or projected about a millimeter. Eggs were more abundant by 20 May, and on 26 May some basal leaves were observed to harbor 50 or more eggs. In a nearby planting that already was in full bloom, eggs were found inserted in sepals.

Nymphs were not present at the sample site on 26 May, but eggs brought back to the laboratory began to hatch within 48 hours. A first-instar nymph was found on rosettes of a nearby colony of *E. vulgare* on 27 May. On 5 June overwintered adults were noticeably less abundant on the plants, eggs were still present, and nymphs, mostly second instars, were observed on flower buds and sepals. Within a week nymphs were restricted to the inflorescences, with instars I–IV present and third instars most numerous. By 18 June only two adults were seen, one probably representing a teneral specimen of the first generation. The nymphal population consisted mainly of fifth instars with third and fourth instars also present. The time required for production of adults in the field (about 35 days) compares well with a developmental time (egg to adult) of 32–38 days recorded in the laboratory at 19°C (Vaysieres, 1983).

On 23 June late-instar nymphs outnumbered first generation adults, which were present on plants with developing flower buds rather than on those with withered inflorescences. A week later adults were common, instars III–V of the first generation were still present, and eggs of a second generation were found in peduncles, bracts, and bracteoles with only a few in midribs of leaves subtending inflorescences. By 8 July first- and second-instar nymphs were common; the single fourth instar collected may have been a "straggler" from the first brood. The numbers of first generation adults appeared to have declined by 16 July; instars I–V were present with some of the late instars possibly representing a first generation. Nymphs of all stages again were present a week later, and first brood adults were now scarce. By 5 August second generation adults, some of them teneral, outnumbered nymphs of this generation (instars IV–V). Leaves subtending inflorescences appeared chlorotic and coated with dark spots of excrement. Most of the plants had turned brown; only a few blossoms remained. On 20 August only two adults and one fifth instar could be collected from the single plant still showing green leaves and bluish inflorescences. Whether second generation adults immediately enter soil near their hosts or disperse to other plants, e.g., pines, is not known. Adults were not found in soil samples taken under basal rosettes of *E. vulgare* at two sites during October.

Observations on *D. echii* made at irregular intervals in other years conformed generally to the 1981 seasonality. In 1982 mating pairs and a few eggs were present by 14 May at the main study site used the previous season; first instars were found on 26 May. At a nearby locality first instars of a second generation were present by 21 June. Plants at the study site had dried up by 20 August 1982, and no tingids were observed. In Pennsylvania adults of this bivoltine species were encountered only occasionally during mid- to late August. Adults and late instars have been collected on 31 August in Erie Co., New York.

The only natural enemy of *D. echii* found in our study was *Sinea diadema* (F.). On an inflorescence of *E. vulgare* an adult of this reduviid was observed feeding on a fifth-instar nymph. In France, Vayssieres (1983) observed another hemipteran

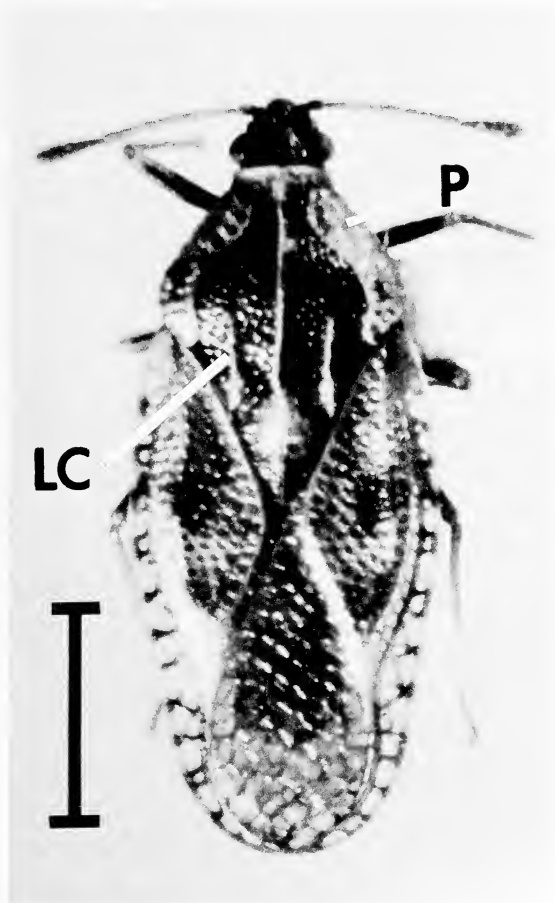


Fig. 1. Adult habitus of *Dictyla echii*. Labelled parts are paranotum (P) and lateral carina (LC); vertical bar = 1.0 mm.

predator, the anthocorid *Orius niger* (Wolff), attacking eggs and first instars of this tingid.

#### RECOGNITION FEATURES

Adults (Fig. 1) of *Dictyla echii*, the only recorded species of the genus *Dictyla* in North America, are easily recognized by the paranota that are broadly reflexed over the pronotum and the shortened lateral carinae of the pronotal disc. This elliptical species, measuring 3.3–3.8 mm long, is further characterized by the black head and pronotum, which strongly contrast with the yellow paranota. The hemelytra are ovoid with the lateral margins evenly convex, mottled dark brown and yellow. Antennal

segments 1 and 2 and the apical segment are black. The femora (except for the apex) and tarsi are dark brown, with the tibiae yellow. The venter is black.

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## SCANNING ELECTRON MICROSCOPIC DEMONSTRATION OF BACTERIA ON TARSI OF *BLATTELLA GERMANICA*

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**Abstract.**—Using scanning electron microscopy (SEM), we have demonstrated the presence of bacteria on the outer surface of the tarsi of adult male and female German cockroaches (*Blattella germanica*), collected from natural populations. Our results indicate that the microorganisms are relatively tightly attached, supporting the hypothesis that mechanical transmission is important in introducing bacteria into human habitation, and may play a role in infections of humans and domesticated animals.

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Various investigators have shown that *Blattella germanica* (Linn.) as well as other species of domesticated cockroaches can transmit infectious diseases. Two mechanical routes by which cockroaches can transport bacteria from waste disposal sites or unsanitary conditions into kitchens where food is prepared have been proposed: 1) adhesion to the exoskeleton, especially on leg surfaces; 2) through the alimentary canal where the organisms can remain viable for several days or weeks and are later expelled (Cornwell, 1968).

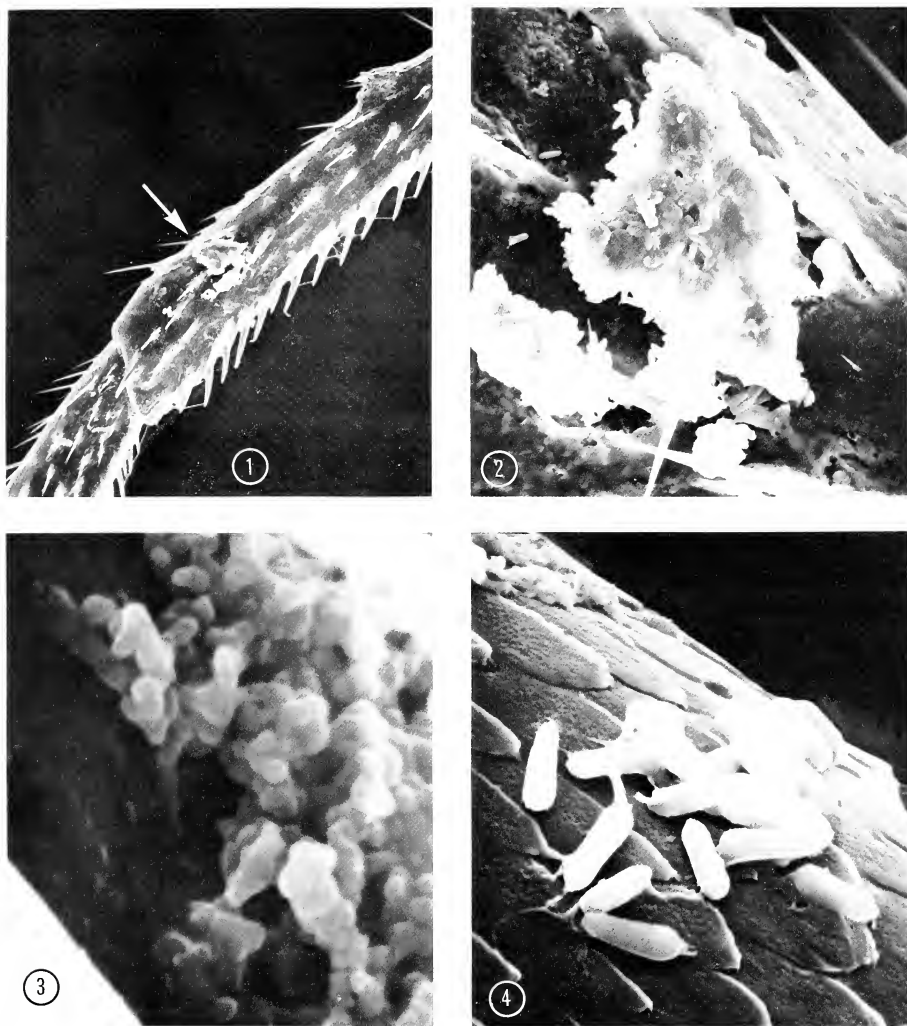
Several investigators have indicated that *B. germanica* serves as primary and developmental vectors for viruses (e.g., poliomyelitis), fungi (*Aspergillus niger*), protozoans (*Entamoeba histolytica*), and helminths (*Raillietiella hemidactyli*, "tongue worms") (Roth and Willis, 1957, 1960; Guthrie and Tindall, 1968; Lavoipierre and Lavoipierre, 1966; Harwood and James, 1979).

The purpose of this study was to determine, using SEM, if bacteria could attach to and colonize the outer surface of the cockroach exoskeleton. Bacterial attachment to and concomitant colonization of the exoskeleton represents a relatively simple route for the mechanical transmission of pathogenic bacteria.

### MATERIALS AND METHODS

Adult *B. germanica* were trapped in large glass jars in an apartment house in New York City. Strips of masking tape were placed on the outer surface of the jar to facilitate cockroach entrance and slices of fresh banana were used as bait. Tarsi of adult male and female cockroaches were prepared for scanning electron microscopy by fixation with 5% glutaraldehyde in 0.067 M phosphate buffer (pH 7.4) for 24 hours at 4°C, and post-fixed with 1% osmium tetroxide in phosphate buffer (pH 7.4) for 1 hr at 4°C. They were then dehydrated for 15 min at room temperature with increasing concentrations of ethanol. The specimens were kept in absolute alcohol and not allowed to dry. Specimens were dried in a Polaron Critical Point Drying Apparatus, Model E 3000, then mounted on brass stubs with double-sided scotch tape, and coated with a 240 Å layer of gold using an ISI-Sputter Coater, Model P. SI (10 mA, 1.2 kV, 4 min; k = 5) (Nowell and Pawley, 1980). Photomicrographs





Figs. 1-4. Attachment of bacteria to the tarsi of *Blattella germanica*. 1. Female, arrow indicates bacilli and associated material ( $\times 100$ ). 2. Enlarged view of area indicated by arrow in Fig. 1. ( $\times 700$ ). 3. Bacterial cocci on male ( $\times 6,000$ ). 4. Bacilli on male ( $\times 3,500$ ).

were taken with Stereoscan Scanning Electron Microscope (JSM-U3) operating at 25 kV.

#### RESULTS

Twenty-five hindleg tarsi from 10 male and 10 female adult *B. germanica* were studied, and bacteria were observed on all specimens. Figures 1 and 2 show that the bacteria were attached to the outer surface of the tarsi and their configuration indicated

colony formation thus suggesting that cockroaches could act as vectors for certain multiplying microorganisms. The micrographs, show that the bacteria are cocci, and rod shaped, and are surrounded by what appears to be a viscous material (Figs. 3 and 4). The presence of this type of substance can facilitate bacterial attachment to a variety of natural environmental surfaces (Bruce et al., 1983). Viscous material constitutes the covering layer or envelope of some bacteria and is known as capsule (integral fibrous glycocalyx) or slime (flexible peripheral glycocalyx) (Bruce et al., 1983; Gibbons, 1977).

#### DISCUSSION

About 40 pathogenic and 45 non-pathogenic species of bacteria have been isolated from naturally contaminated cockroaches (Roth and Willis, 1957). Many of the pathogens were isolated from *B. germanica*. An important feature in mechanical bacterial transmission is the fact that some microorganisms can remain viable on inert surfaces for long periods. *Salmonella oranienburg* (which has been found naturally in cockroaches) can survive at room temperature for up to 34 days on an inert surface such as glass, and will remain viable for at least 62 and 88 days when attached to corn flakes, and dry biscuits, respectively (Cornwell, 1968). Roth and Willis (1957, 1960) indicate that the evidence implicating cockroaches in the transmission of bacterial disease agents is largely circumstantial. Scanning the tarsi with SEM provides direct evidence that bacteria can attach and colonize the cockroach exoskeleton. This attachment permits mechanical transmission which may be of significance in certain bacterial infections affecting humans and domesticated animals. Although surface attachment and colonization is widespread in nature, little is known about the mechanisms involved in the adhesion of microorganisms to surfaces (Gibbons, 1977; Beachey, 1981; Galask et al., 1984).

#### ACKNOWLEDGMENTS

We thank Dr. T. Koyama for providing microscope time at the New York Botanical Garden and Dr. F. Herz for assisting with the manuscript. This project was conducted as a course requirement for BI65001 Medical Entomology at Fordham University.

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## PARASITISM AND MORTALITY CAUSED BY FIELD AND LABORATORY STRAINS OF *BRACHYMERIA INTERMEDIA* (NEES) (HYMENOPTERA: CHALCIDIDAE)

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**Abstract.**—A laboratory strain of *Brachymeria intermedia* (Nees), which has been in culture for several years and a field strain were examined for differences in parasitic activity. The gypsy moth pupae were exposed to the wasp for 30, 60, 90 and 120 min. In the latter three time periods the laboratory strain visited significantly more hosts than the field strain. In the two shortest time periods the field strain parasitized significantly more hosts. However, total mortality was the same for both strains. Possible reasons for the similarity in mortality are discussed.

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The most recent outbreak of gypsy moth, *Lymantria dispar* L. in the northeastern United States and expansion of its range into Maryland and central Pennsylvania hardwood forests continues to stimulate interest in the development of an integrated pest management system for this insect. Because of public concern from insecticide spraying near homes, one potential tactic is augmentative releases of gypsy moth natural enemies in suburban woodlots.

*Brachymeria intermedia* (BI) has been a candidate for augmentative release because it is relatively easy to rear. The wasp is a polyphagous parasitoid but its principal host is the gypsy moth (Dowden, 1935). Its initial introduction into the United States was in 1918 from material collected in France and Italy (Howard and Fiske, 1911). Subsequently, no recoveries of the wasp were reported until Burks (1960) found a pinned specimen that had been collected in 1942. Another release of BI was made in Connecticut in 1963 and Leonard (1966, 1967) reported establishment in Connecticut and Maine. The wasp is established throughout the northeastern United States. An augmentative release program requires use of wasps that are competitive in the field, so the purpose of this study was to find if there were differences in behavior or actual parasitism of newly cultured strain of BI and one that had been in culture the New Jersey Department of Agriculture (NJDA) since 1966.

### MATERIALS AND METHODS

Collection of field strain BI was made by the New Jersey Department of Agriculture in the summer of 1981 from a heavily defoliated site of predominately oak. The subsequent colony was maintained continuously on gypsy moth pupae through the time of this experiment (1982). The laboratory strain has been maintained at various intervals on gypsy moth and the greater wax moth (*Galleria mellonella* L.) since 1966. For three generations prior to this experiment, both strains of BI were reared solely on gypsy moth pupae. Laboratory conditions were maintained between 21–23°C; 46–48% RH and a 16:8 LD cycle.

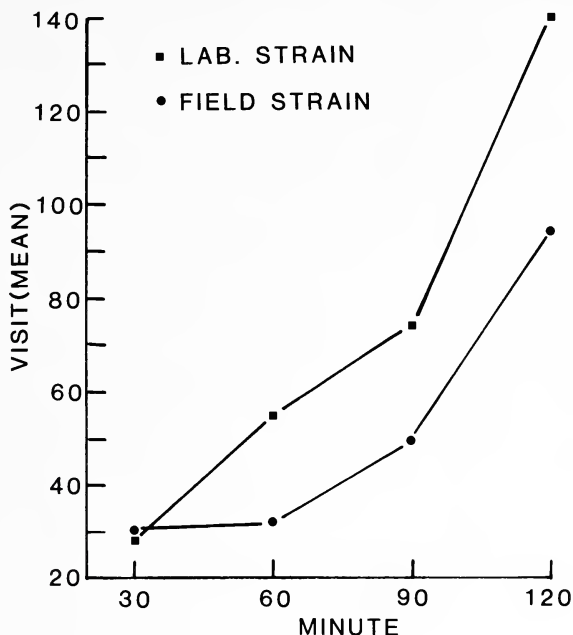


Fig. 1. Mean number of visits by a laboratory or field strain of *Brachymeria intermedia* (Nees) to 20 three to four-day-old gypsy moth pupae over a 30, 60, 90 or 120 min exposure period.

Twenty (5 cm diam) plastic condiment cup lids were spaced evenly on 20.3 × 27.9 cm cardboard sheets and fixed with Elmers glue. The cardboard sheets with attached lids were then placed in the bottom of a 34 × 34 × 40 cm wood and screen cage with a sliding glass door. One, 3 to 4 day old, female gypsy moth pupa was placed on each lid; then 20 five to seven day old mated female BI's were introduced into the cage. To examine for differences in BI activity relative to exposure time, we used 30, 60, 90 and 120 min exposures of the wasp to the pupae. During the exposure period the number of BI landing (visits) was recorded for 1 min in every 5 min. Due to the size of the cage we were only able to determine if a female was sitting on a pupa. After the exposure was complete, the pupae were placed individually in 29.5 ml plastic cups and observed daily for emergence of a moth or parasitoid. Pupae from which nothing emerged were dissected to determine the cause of mortality. If the pupae contained any stages of BI it was calculated as successful parasitism. On each of the 13 days that an experiment was conducted, 20 unexposed pupae were held during the experimental period and placed individually in condiment cups to account for natural mortality.

#### RESULTS AND DISCUSSION

Adults emerged from all unexposed pupae that were held during the experiments emerged in to adults so no correction due to natural mortality is necessary.



Table 1. Mean response of a field strain and laboratory strain of *Brachymeria intermedia* Nees after exposure to 20 2–4-day-old gypsy moth pupae for 30, 60 or 120 min.\*\*

Min		30	60	90	120
No. of replicates	FS	8	7	5	5
	LS	7	9	5	5
% parasitism	FS	46.7 (0.8)a	50.7 (8.40)a	58.0 (1.3)a	70.0 (14.4)a
	LS	32.9 (1.3)b	36.7 (14.5)b	52.0 (2.8)a	67.0 (11.0)a
% apparently killed by feeding	FS	16.3 (5.2)a	13.2 (6.90)a	16.0 (0.6)a	21.3 (7.4)a
	LS	27.9 (0.1)b	26.1 (12.7)b	25.0 (0.3)b	19.0 (4.2)a
Total % mortality	FS	63.2 (0.9)a	64.3 (6.10)a	74.0 (7.40)a	91.3 (9.2)a
	LS	60.7 (2.0)a	62.8 (19.4)a	77.0 (21.4)a	86.0 (7.4)a
Sex ratio F:M	FS	1:2.95	1:4.07	1:2.87	1:5.22
	LS	1:0.41	1:0.57	1:0.63	1:0.43

\* Number in parentheses equals + 1 SD.

\*\* Within each factor and each time period if a mean is not designated by the same letter it is significantly different ( $P < 0.05$ ).

Examination of the raw data revealed that all pupae were visited at least once and Figure 1 shows that both strains visited an average of 30 pupae during the 30 min exposure period. So, individuals of both strains were sufficiently active in this time period to begin the host recognition–acceptance process (sensu Doult, 1964). The 60, 90 and 120 min exposures resulted in the laboratory strain visiting significantly more pupae than the field strain ( $P < 0.05$  in each). From the 30 to 120 min period the laboratory strain increased from just over 1.5 visits/pupa to 7 visits/pupa while the field strain increased from slightly over 1.5 pupa at 30 min to 5/pupa at 120 min.

High parasitism per female is the desired result in a mass rearing program and ultimately reflects on the parasitoids ability to search for and find a host. Table 1 shows that the field strain in shorter exposure periods (30–60 min) successfully parasitize more hosts than the laboratory strain. At the 30 min exposure the field strain parasitized 46.7% of the hosts while the laboratory strain parasitized only 32.9% ( $P < 0.05$ ). The magnitude of the differences in parasitism between the two strains remained similar at the 60 min exposure period; the field strain parasitized 50.7% of the hosts and the laboratory strain parasitized 36.7% ( $P < 0.05$ ). At the longer exposure periods (90–120 min) there were no significant differences in successful parasitism between the two strains.

Another behavioral difference between the laboratory and field strains is the amount of host killing by feeding on host fluids. Under close scrutiny of the wasp in the laboratory we observed this behavior and Rotheray et al. (1984) also report this behavior. Due to the size of the experimental cage, we were unable to collect empirical data on feeding, however since no unexposed pupae died, and many exposed pupae were dehydrated, we assign the cause to dehydration to feeding by BI. The laboratory strain killed nearly twice the number of pupae in this manner than the field strain at 30, 60, and 90 min ( $P < 0.05$  for each). But at the 120 min exposure this cause

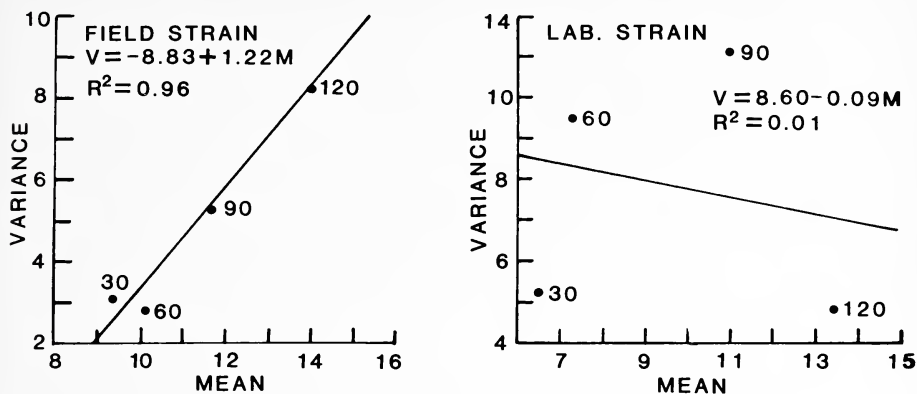


Fig. 2. Mean-variance ratio of actual parasitism by *Brachymeria intermedia* (Nees) or 20 gypsy moth host in a 30, 60, 90 or 120 min exposure period.

of mortality was statistically similar for pupae exposed to either of the two strains (Table 1). Interestingly enough, the killing power (no. BI + no. fed upon) is the same for both strains at each exposure period (Table 1). The number killed ranged from 60% at 30 min to roughly 90% after 120 min. Because of the high visitation rate by the laboratory strain, we attribute these results to a gradual selection for a longer handling time in the rearing laboratory.

Figure 2 shows the mean-variance ratio of the number of BI emerging/replicate for each strain at each exposure period. With the field strain the variance increases with the mean in a linear fashion indicating that parasitism by BI was randomly distributed within the replicates (Southwood, 1978). The laboratory strain mean-variance ratio does not increase with the mean indicating that the ability of BI to parasitize the host does not follow a random distribution. That is, in the years that the laboratory strain has been in culture selection has been for wasps with a longer handling time resulting in non-random parasitism in the laboratory. Aggressiveness is of primary importance when culturing parasitoids. We argue that the longer time for successful parasitism by the laboratory strain could diminish effectiveness of the wasp in an augmentative release program, especially in light of the host defenses described by Rotheray et al. (1984).

Hoy (1976) stated that genetic deterioration of laboratory cultures is difficult to circumvent. In a mass rearing facility, conditions for selection of an increased handling time is difficult to avoid because too short exposure time will result in poor reproduction of the parasitoid thus increasing production costs. The tendency then is to increase exposure time to yield higher numbers of wasps.

Another trade off to be considered in a rearing program is maintenance of a favorable sex ratio. Both for insects used in a laboratory production colony and those intended for field release, it would be more cost effective to have a high female to male sex ratio. In this study, the laboratory strain had a more favorable sex ratio by producing 2 to 2.5 more females than males (Table 1). Exposures of the field strain to gypsy moth pupae produced a range from 3 to 5 males to females. Declining female to male sex ratio greatly increases production costs. We conclude that annual re-

stocking of laboratory cultures in spite of its attendant annual costs of diminished female returns/unit effort remains a worthy effort.

#### ACKNOWLEDGMENTS

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## NOTES ON THE SPIDER GENUS *EILICA* (ARANEAE: GNAPHOSIDAE)

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**Abstract.**—The genus *Baeriella* Simon is transferred from the Cybaeodinae (Clubionoidea) to the Laroniinae (Gnaphosidae) and newly synonymized with *Eilica* Keyserling; its type species, *B. myrmecophila* Simon, is placed as a senior synonym of *Eilica puno* Platnick and Shadab. Three new species are described: *E. amambay* from Paraguay and *E. daviesae* and *E. bedourie* from Australia. The male of *E. contacta* Platnick is described for the first time.

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The spider genus *Eilica* is of particular interest both because of its widespread, Gondwanian distribution (Platnick, 1975) and because of the close associations that apparently exist between at least some of its species and ants (Noonan, 1982). The sister group of *Eilica*, the Laurasian genus *Callilepis* (Platnick, 1976b), includes at least some species that seem to feed exclusively on ants (Heller, 1976).

Because *Eilica* has such a wide distribution, it is not surprising that different generic names have been used for species living on different continents. Earlier studies (Platnick, 1975; Platnick and Shadab, 1981) have placed five generic names (*Gytha* Keyserling, *Laronia* Simon, *Gnaphosoides* Hogg, *Caridrassus* Bryant, and *Fedotovia* Charitonov) as junior synonyms of *Eilica*, although the synonymy of the last of these names has yet to be confirmed by examination of its type species. During a recent visit to the Muséum National d'Histoire Naturelle, Paris, I discovered yet another generic synonym, *Baeriella* Simon (1903), based on a myrmecophilous species from Argentina overlooked in previous studies because all recent workers and catalogers have associated the genus with clubionoid rather than gnaphosoid spiders. Simon had assigned *Baeriella*, along with the Mediterranean genus *Cybaeodes* and the African genus *Andromma*, to his gnaphosid subfamily Cybaeodinae. As indicated elsewhere (Platnick, 1984), this subfamily was correctly removed from the Gnaphosidae by subsequent workers (although its correct position remains uncertain). Simon's association of *Baeriella* with *Cybaeodes* and *Andromma*, however, was erroneous. Examination of Simon's type specimens indicates that *Baeriella myrmecophila* is a true gnaphosid and a senior synonym of *Eilica puno* Platnick and Shadab, a species previously found only living with ants in the Peruvian Andes.

In addition to recording this synonymy, I take the opportunity here to describe previously unknown taxa and list new locality records for known *Eilica* species, based on material new to the collections of the American Museum of Natural History (AMNH) or kindly made available by the following curators and collectors: Dr. A. Timotheo da Costa, Museu Nacional, Rio de Janeiro (MNRJ); Dr. V. E. Davies, Queensland Museum, Brisbane (QMB); Mr. P. Hillyard, British Museum (Natural History), London (BMNH); Mr. M. Hubert, Muséum National d'Histoire Naturelle, Paris (MNHN); Dr. H. W. Levi, Museum of Comparative Zoology, Cambridge

(MCZ); Dr. A. A. Lise, Museu de Ciências Naturais, Porto Alegre (MCN); Dr. V. Mahnert, Muséum d'Histoire Naturelle, Geneva (MHNG); Dr. E. A. Maury, Museo Argentino de Ciencias Naturales, Buenos Aires (MACN); and Dr. L. E. Watrous, Field Museum of Natural History, Chicago (FMNH). The illustrations are by Dr. M. U. Shadab of the American Museum. The format of the descriptions follows that of Platnick (1975).

### *Eilica* Keyserling

*Eilica* Keyserling, 1891:29 (type species by monotypy *Eilica modesta* Keyserling). Platnick, 1975:3. Platnick and Shadab, 1981:184.

*Baeriella* Simon, 1903:271 (type species by monotypy *Baeriella myrmecophila* Simon). **New Synonymy.**

**Synonymy.** Specimens of *Baeriella myrmecophila* possess the multiple cheliceral laminae (Fig. 1) diagnostic of *Eilica*.

### *Eilica myrmecophila* (Simon), **New Combination**

Fig. 1

*Baeriella myrmecophila* Simon, 1903:272, figs. A–C (seven female syntypes from Lara, Tucuman, Argentina, in MNHN, examined).

*Eilica puno* Platnick and Shadab, 1981:185, figs. 7, 8 (female holotype from Puno, Puno, Peru, in AMNH, examined). **New Synonymy.**

**Diagnosis.** The shield-shaped epigynum (Platnick and Shadab, 1981, fig. 7) is diagnostic of females, as is the peculiarly elongated medial cheliceral lamina (Fig. 1).

**Male.** Unknown.

**Female.** Described by Simon (1903) and Platnick and Shadab (1981).

**Distribution.** Simon's specimens were collected at an elevation of 4,000 m in the Argentine Andes by G.-A. Baer, where they were found (together with their characteristically shaped egg cases) living with the ant *Camponotus punctulatus* Mayr. Platnick and Shadab's specimens were collected at an elevation of 3,850 m in the Peruvian Andes by G. R. Noonan and M. Moffett, living with the ant *Camponotus inca* Emery, as detailed by Noonan (1982).

**Synonymy.** Although the Argentine specimens are lighter in coloration than the Peruvian ones, no structural differences have been detected between them.

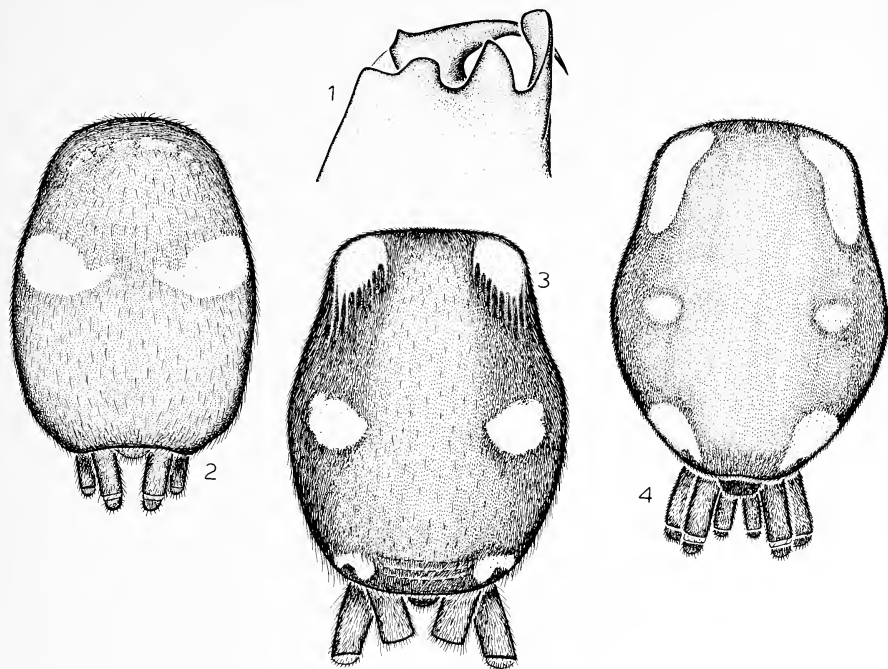
### *Eilica modesta* Keyserling

*Eilica modesta* Keyserling, 1891:30, pl. 1, figs. 9, 9a, 9b (male holotype from Blumenau, Santa Catarina, Brazil, should be in BMNH, lost). Platnick, 1975:6, figs. 3, 8–11; 1977:397.

*Zelotes pallidenotatus* Mello-Leitão, 1938:113, figs. 32, 33 (female holotype from Roca, Río Negro, Argentina, in Museo de La Plata, examined). First synonymized by Platnick and Shadab, 1983:101.

**New records.** **Argentina:** Jujuy: Abra Pampa, Feb. 1966 (E. A. Maury, MACN), 1♀. **San Juan:** Valle Fértil, Caucete, Oct. 1980 (M. E. Galiano, MACN), 1♀. **Brazil:**





Figs. 1-4. 1. *Eilica myrmecophila* (Simon), tip of chelicera, ventral view. 2-4. Dorsal view of abdomen. 2. *E. amambay*, new species. 3. *E. daviesae*, new species. 4. *E. bedourie*, new species.

*Minas Gerais*: 20 mi N Governador Valadares, Mar. 24, 1984, under rock on sandy streamside (L. N. Sorkin, AMNH), 1♀. *Santa Catarina*: Blumenau (M. Witte, MCZ), 1♀.

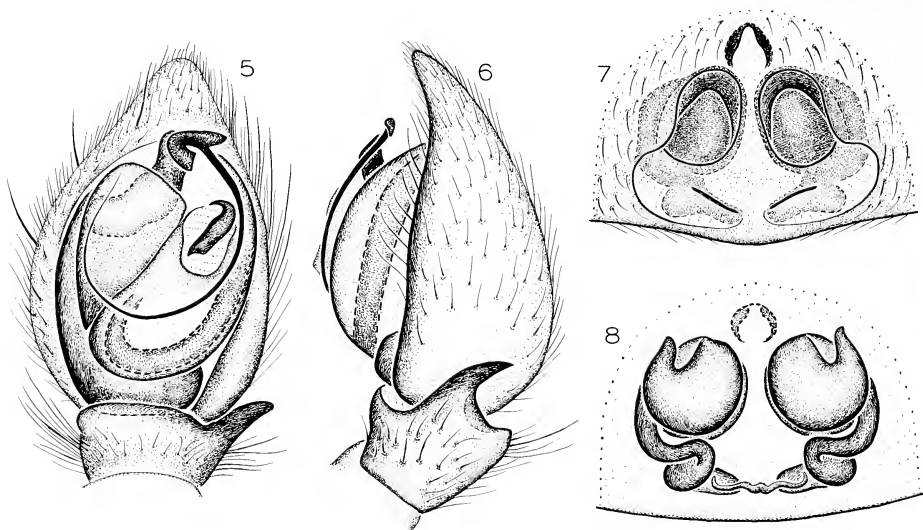
*Distribution*. Argentina, Uruguay, and southeastern Brazil.

*Eilica trilineata* (Mello-Leitão)

*Laronia trilineata* Mello-Leitão, 1941:173, fig. 63 (female holotype from Alemania, Salta, Argentina, should be in Museo de La Plata, lost).

*Eilica trilineata*: Platnick, 1975:6, figs. 14, 15. Platnick and Shadab, 1981:185, figs. 1, 2.

*New records*. **Argentina**: *Chubut*: Los Cipreses, Nov. 1982 (Ramirez, MACN), 6♂♂, 1♀. *Salta*: Juramento (MNRJ), 1♀. **Brazil**: *Rio Grande do Sul*: Estação Ecológica Aracurí, Esmeralda, Dec. 13, 1978 (C. J. Becker, MCN), 1♀. **Chile**: *Bío-Bío*: 2-5 km E El Abanico, Nov. 20-21, 1981, elevation 760-975 m, under rocks on scrubby mountainside (N. I. Platnick, R. T. Schuh, AMNH), 3♀♀. *Curicó*: Los Queñes, Jan. 1984 (E. A. Maury, MACN), 1♀. *Ñuble*: Las Trancas, Nov. 15, 1981, elevation 1,280 m, under rocks in scrubby valley below beech forest (N. I. Platnick, R. T. Schuh, AMNH), 3♀♀; 40 km W Las Trancas, Nov. 15, 1981, elevation 1,370 m, under rock in scrubby valley (N. I. Platnick, R. T. Schuh, AMNH), 1♀; 10 km W Termas de



Figs. 5–8. *Eilica amambay*, new species. 5. Palp, ventral view. 6. Palp, retrolateral view. 7. Epigynum, ventral view. 8. Epigynum, dorsal view.

Chillán, Nov. 14, 1981, elevation 1,200 m, under rock in low beech forest (N. I. Platnick, R. T. Schuh, AMNH), 1♀.

*Distribution.* Chile, Argentina, and southeastern Brazil.

*Eilica uniformis* (Schiapelli and Gerschman)

*Laronia uniformis* Schiapelli and Gerschman, 1942:330, figs. 17–19 (female holotype from Colonia Dora, Santiago del Estero, Argentina, in MACN, examined).

*Eilica uniformis*: Platnick, 1975:9, figs. 18, 19.

*New record. Argentina: Misiones:* Yawi, Dec. 3–9, 1972 (E. A. Maury, MACN), 1♀.

*Distribution.* Known only from Argentina.

***Eilica amambay*, new species**

Figs. 2, 5–8

*Type.* Male holotype from forest litter in the Parque Nacional Cerro Corá, Amambay, Paraguay (May 29–31, 1982; J. A. Kochalka), deposited in AMNH.

*Etymology.* The specific name is a noun in apposition taken from the type locality.

*Diagnosis.* The laterally directed spur at the base of the embolus of males (Fig. 5) and the anteriorly narrowed lateral epigynal margins of females (Fig. 7) are diagnostic.

*Male.* Total length 2.25–2.45. Carapace 1.01–1.15 long, 0.79–0.86 wide. Femur II 0.65–0.75 long (three specimens). Carapace dark olive brown; abdomen dark gray with white spots (Fig. 2); coxae and trochanters yellow on posterior legs, slightly darker on anteriors, femora dark brown, patellae light brown proximally, dark brown

distally, tibiae dark brown, metatarsi and tarsi brownish orange. Eye sizes and interdistances: AME 0.05, ALE 0.06, PME 0.07, PLE 0.06; AME-AME 0.04, AME-ALE 0.01, PME-PME 0.05, PME-PLE 0.04, ALE-PLE 0.04; MOQ length 0.13, front width 0.14, back width 0.18. Embolar base bearing laterally directed spur (Fig. 5); retrolateral tibial apophysis short, sharp (Fig. 6). Leg spination: femur IV p0-0-1, r0-0-0; tibiae: I v1p-1p-2; IV v0-0-2, r0-1-1; metatarsus IV p0-0-0, v1p-0-2, r0-0-1.

**Female.** Total length 2.74. Carapace 1.19 long, 0.85 wide. Femur II 0.76 long. Coloration as in male except metatarsus IV dark brown. Eye sizes and interdistances: AME 0.05, ALE 0.07, PME 0.06, PLE 0.07; AME-AME 0.05, AME-ALE 0.02, PME-PME 0.06, PME-PLE 0.05, ALE-PLE 0.05; MOQ length 0.15, front width 0.15, back width 0.18. Lateral epigynal margins abruptly narrowed anteriorly (Fig. 7); spermathecae bipartite (Fig. 8). Leg spination: femur II p0-0-0; tibiae: I v1p-1p-2; III, IV p0-0-1; metatarsi: II v1p-0-2; III, IV p0-0-0.

**Other material examined.** **Paraguay:** *Caaguazú:* 20 km N Colonel Oviedo, Oct. 8, 1979 (V. Mahnert, MHNG), 1♂. *Canindiyu:* Itanará, Oct. 27, 1979, elevation 430 m (V. Mahnert, MHNG), 1♀. **Central:** San Lorenzo, Sept. 20-30, 1982 (J. A. Kochalka, AMNH), 1♂. **Paraguarí:** Parque Nacional Ybyouí, Sept. 3-4, 1984 (J. A. Kochalka, AMNH), 1♂.

**Distribution.** Known only from Paraguay.

### *Eilica tikaderi* Platnick

*Eilica tikaderi* Platnick, 1976a:189, figs. 1, 2 (female holotype from Pashan, Poona, Maharashtra, India, in Zoological Survey of India, examined). Platnick and Shadab, 1981:184, figs. 9, 10. Tikader, 1982:342, figs. 108-113.

**New records.** **India:** *Mysore:* Bangalore (P. P. Staunton, BMNH), 1♀. *West Bengal:* Calcutta, Nov. 1958 (N. L. H. Krauss, AMNH), 1♀.

**Distribution.** Known only from India.

### *Eilica albopunctata* (Hogg)

*Gnaphosoides albopunctata* Hogg, 1896:333, fig. 18 (male holotype from Storm Creek, South Australia, in National Museum of Victoria, examined).

*Eilica albopunctata:* Platnick, 1975:14, figs. 6, 28, 29; 1978:226, figs. 1-3.

**New records.** **Australia:** *Queensland* (mideastern): Barracks, Upper Dry Creek, Kroombit Tops, 45 km SSW Calliope, Dec. 9-19, 1983, open sclerophyll forest on sandstone plateau (Monteith, Davies, Gallon, Thompson, QMB), 1♂; (southwestern): Jumbo Bore, Norley, Thargomindah, Sept. 28, 1983, pitfall traps around sub-artesian bore tank and overflow pond surrounded by molga red earth (B. R. Jahnke, QMB), 1♂; 55 km NW Bedourie, Oct. 16-23, 1979, pitfall traps, stony plain (S. Morton, QMB), 1♂. *Western Australia:* Wannamal, Nov. 11, 1976, under debris on flood plain with *Idiomyrex* present (J. Kethley, FMNH), 1♂.

**Distribution.** Known only from Australia (Queensland, South Australia, and Western Australia).

*Eilica serrata* Platnick

*Eilica serrata* Platnick, 1975:18, figs. 2, 7, 32, 33 (male holotype from Geraldton, Western Australia, in MCZ, examined); 1978:226, figs. 4-6.

**New record. Australia: Queensland** (southeastern): Mulgowie, Mar. 10, 1981, pitfall trap, sclerophyll (M. D. Grant, QMB), 1♀.

**Distribution.** Known only from Australia (southern Queensland and Western Australia).

*Eilica contacta* Platnick

Figs. 9, 10

*Eilica contacta* Platnick, 1975:15, figs. 34, 35 (female holotype from Dorriggo, New South Wales, Australia, in MCZ, examined).

**Diagnosis.** The large, scoop-shaped spur on the embolar base (Figs. 9, 10) is diagnostic of the male, which is matched here with *E. contacta* (previously known from females only) primarily on the basis of size and coloration, and which may therefore actually belong to an undescribed species instead.

**Male.** Total length 2.61. Carapace 1.22 long, 0.90 wide. Femur II 0.77 long. Carapace light brown; abdominal pattern indeterminate due to poor preservation; coxae light yellow, femora brown except for yellow proximal quarter of femur IV, patellae and tibiae light brown, metatarsi and tarsi brownish orange. Eye sizes and interdistances: AME 0.03, ALE 0.06, PME 0.05, PLE 0.07; AME-AME 0.06, AME-ALE 0.02, PME-PME 0.06, PME-PLE 0.05, ALE-PLE 0.05; MOQ length 0.15, front width 0.12, back width 0.15. Embolar base bearing large scoop-shaped spur (Fig. 9); retrolateral tibial apophysis oblique (Fig. 10). Leg spination: femur III p0-0-0; tibiae: I v1p-1p-2; II v1p-2-2; III v1p-2-2; IV p1-1-1; metatarsi: III p1-1-1, r0-1-1; IV p0-1-1, v0-2-2, r1-1-0.

**Female.** Described by Platnick (1975).

**New records. Australia: Queensland** (mideastern): Northern Escarpment, Kroombit Tops, 45 km SSW Caliope, Dec. 11-18, 1983, pitfall, open sclerophyll forest on sandstone plateau (Monteith, Davies, Gallon, Thompson, QMB), 2♀♀; (southwestern): 55 km NW Bedourie, Aug. 7-13, 1980, pitfall trap, stony plain (S. Morton, QMB), 1♂.

**Distribution.** Known only from Australia (Queensland and northern New South Wales).

*Eilica daviesae*, new species

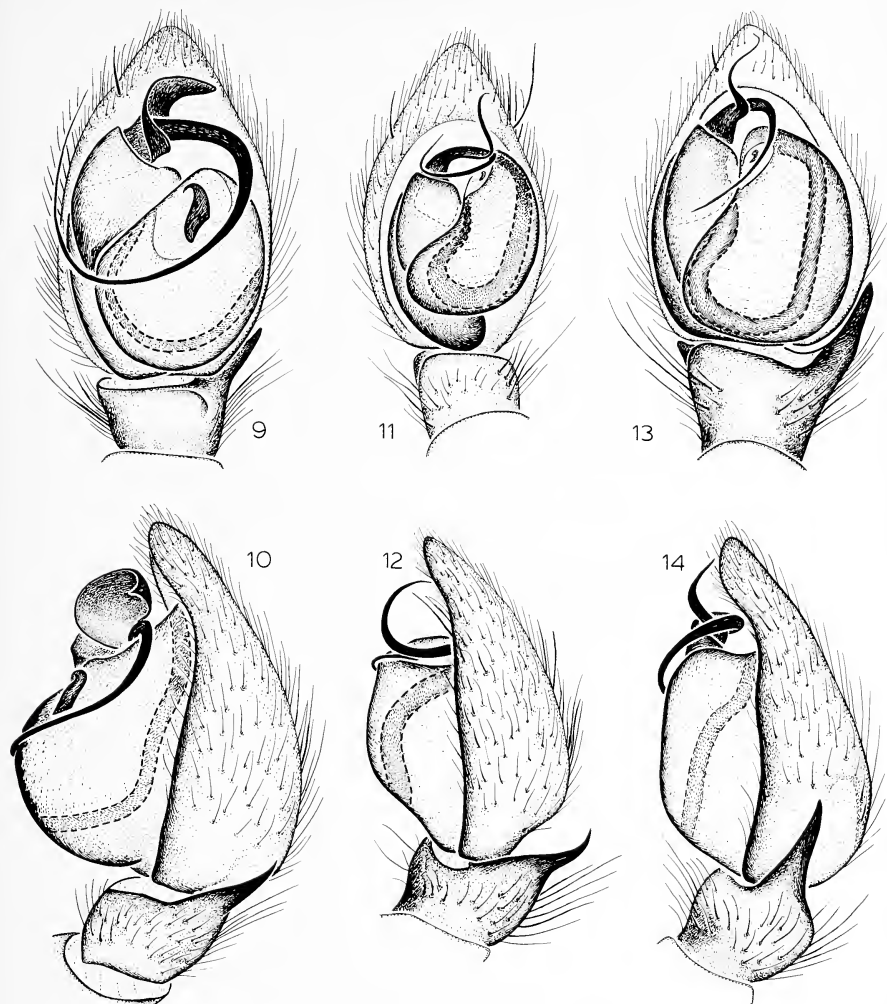
Figs. 3, 11, 12

**Type.** Male holotype from a pitfall trap along dry gully in sparse mulga land at Central Tank, "Orient," in the Grey Range of southwestern Queensland, Australia (September 1983; B. R. Jahnke), deposited in QMB.

**Etymology.** The specific name is a patronym in honor of Dr. Valerie Davies of the Queensland Museum, who first recognized the species.

**Diagnosis.** This small species seems most closely related to *E. bedourie*, new species,





Figs. 9–14. 9, 10. *Eilica contacta* Platnick. 11, 12 *E. daviesae*, new species. 13, 14. *E. bedourie*, new species. 9, 11, 13. Palp, ventral view. 10, 12, 14. Palp, retrolateral view.

with which it shares the long, sinuous spur at the embolar base (Fig. 11), but can be distinguished by the dorsally directed retrolateral tibial apophysis (Fig. 12).

*Male*. Total length 1.89. Carapace 0.94 long, 0.79 wide. Femur II 0.65 long. Carapace brown with darker reticulations; abdomen black with white markings (Fig. 3); legs brown with tarsi lightened. Eye sizes and interdistances: AME 0.04, ALE 0.06, PME 0.04, PLE 0.07; AME–AME 0.04, AME–ALE 0.03, PME–PME 0.04, PME–PLE 0.05, ALE–PLE 0.08; MOQ length 0.11, front width 0.11, back width 0.12. Embolus short, weak, bearing long, sinuous spur at base (Fig. 11); retrolateral



tibial apophysis relatively long, directed dorsally (Fig. 12). Leg spination: tibia III d1-0-0, r0-0-1; metatarsi: I, II v1r-0-2; III v1p-0-2; IV v1p-1p-2, r0-0-0.

*Female.* Unknown.

*Other material examined.* None.

*Distribution.* Known only from southwestern Queensland.

***Eilica bedourie*, new species**

Figs. 4, 13, 14

*Type.* Male holotype from a pitfall trap on a sandy ridge 55 km northwest of Bedourie, southwestern Queensland, Australia (June 6–12, 1980; S. Morton), deposited in QMB.

*Etymology.* The specific name is a noun in apposition taken from the type locality.

*Diagnosis.* This small species seems closest to *E. daviesae*, new species, but can be distinguished by the distally directed retrolateral tibial apophysis (Fig. 14).

*Male.* Total length 2.41. Carapace 0.93 long, 0.77 wide. Femur II 0.73 long. Carapace light brown with darker reticulations; abdomen brownish gray with white markings (Fig. 4); legs light brown with metatarsi and tarsi lightened. Eye sizes and interdistances: AME 0.03, ALE 0.05, PME 0.04, PLE 0.06; AME–AME 0.04, AME–ALE 0.03, PME–PME 0.05, PME–PLE 0.04, ALE–PLE 0.11; MOQ length 0.12, front width 0.10, back width 0.13. Embolus short, weak, bearing long, sinuous spur at base (Fig. 13); retrolateral tibial apophysis relatively long, directed distally (Fig. 14). Leg spination (tibiae and metatarsi III and IV missing): tibiae: I p1-0-1, v0-1r-2; II p0-0-1, v0-1r-2.

*Female.* Unknown.

*Other material examined.* None.

*Distribution.* Known only from southwestern Queensland.

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LARVAL CHARACTERS OF A NEOTROPICAL *SCOTOCRYPTUS*  
(COLEOPTERA: LEIODIDAE), A NEST ASSOCIATE OF  
STINGLESS BEES (HYMENOPTERA: APIDAE)

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*Abstract.*—Late instar larvae of a Neotropical species of *Scotocryptus*, tentatively identified as *S. meliponae* Girard and associated with adults determined as that species (Coleoptera: Leiodidae) are described from the nest of a stingless bee (Hymenoptera: Apidae: Meliponinae) in Manaus, Brazil. Habitus drawings and illustrations of selected characters are given to facilitate recognition of scotocryptine larvae and several characters are suggested to be adaptive apomorphs related to inquilinism, including dorso-ventral body compression, loss of stemmata, presence of stout spines, porelike cuticular structures, and an inverse c-shaped curvature of the body.

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Scotocryptine beetles (Coleoptera: Staphylinoidea: Leiodidae) have been known inhabitants of nests of Neotropical stingless bees for more than a century (Girard, 1874), but details of this association remain enigmatic. Taxonomic, ecological, and behavioral studies are needed for all four genera of the Scotocryptini that are associated with Meliponinae (Hymenoptera: Apidae) (Portevin, 1907, 1937; Wheeler, 1979). Available evidence suggests that these beetles are scavengers in nests of host bees, feeding on feces and fungal spores and hyphae that are present (Salt, 1929; Wilson, 1971; Roubik and Wheeler, 1982); an interesting departure from epigeal mycophagy in the related genera *Creagrophorus* and *Aglyptinus* (Newton, 1984; Wheeler, 1979, 1984). Adult structural peculiarities and phoretic behavior have been described by Roubik and Wheeler (1982).

There have been few published works on larvae of scotocryptines inhabiting bee nests, or their free-living relatives (Paulian, 1941; Peyerhimhoff, 1907; Wasmann, 1904; Wheeler, 1979). In this paper, I describe late instar larvae of *Scotocryptus meliponae* Girard and discuss some apomorphs apparently adaptive for inquilinism. These remarks, and accompanying figures, should facilitate recognition and collection of additional specimens, provide a basis for comparisons as more data are acquired, and suggest some structural details in need of further study.

MATERIALS AND METHODS

I have been able to study only a single series of four larvae of *S. meliponae*. These late (probably third) instar larvae were collected by D. W. Roubik and F. Perolta at Manaus, Brazil on May 7, 1981. Habitus drawings were made from a critical point dried specimen mounted on a point using a Wild M5A dissecting microscope with a drawing-tube. Detailed drawings were made from a slide mounted individual using a Leitz compound microscope equipped with interference contrast illumination and a drawing attachment. These two specimens, and a third in alcohol, are in the Cornell

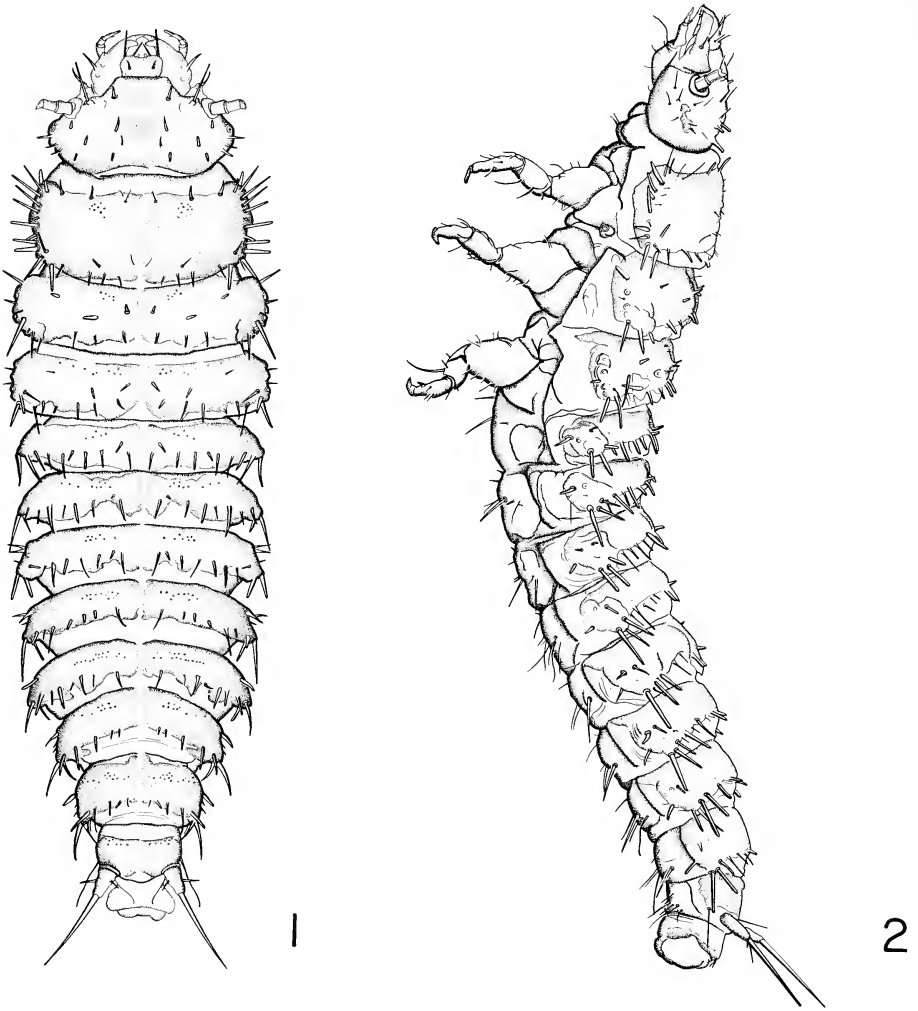
University Insect Collection. A fourth specimen (in alcohol) has been deposited in the Museum National d'Histoire Naturelle (Paris). I have used the term "pore" as a matter of convenience, as it has been used previously (e.g., Wheeler and Pakaluk, 1983), although some of these structures may be campaniform sensillae as suggested by Ashe and Watrous (1984). The special tergal "pores" discussed under adaptations, however, are not such sensillae.

#### DESCRIPTION OF LARVAL *Scotocryptus meliponae*

*General features.* Late instar larva. Body elongate, broad, somewhat dorso-ventrally flattened (Figs. 1, 2). Dorsum with many stout setae. Color creamy white (in ethanol). Length 7.4 mm distended.

*Head.* Head capsule broad (width/length = 1.5). Stemmata absent. Dorsal surface with small, simple setae; larger, blunt, fluted setae; and larger, lateral, fimbriate setae (approximate number and placement shown in Fig. 3); integument with crenulate microsculpture. Ventral surface with fewer, simple setae, except those at lateral margins. Antenna short; antennomere I (width/length = 0.8) with two dorsal pores; II more elongate (width/length = 0.53), ventral surface with imbricate scales, seta near apex, large oval sensillum in apical membrane, apicolateral seta, and small subapical sensillum and pointed cuticular process in membrane; III small (width/length = 1.0), with single dorsal sensillum, two ventral apicolateral sensillae (Fig. 5). Labrum with 2 large setae on disc, 2 large lateral setae; apical margin with 4 large, 2 small, and 2 minute setae; ventral surface with 2 subapical setae, apicolateral patches of microtrichiae, and 2 minute setae near middle subapically (Fig. 4). Mandible stout; apex with 2 large and 3 smaller dens; mola heavily sclerotized, not prominent, with poorly defined transverse ridges, each minutely crenulate; tooth at middle with point and crenulate edge; circular pit on ventral surface near medial tooth, with about a dozen long, fine setae (Figs. 6, 7). Maxilla elongate, narrow; mala undifferentiated, with fine setae along basal portion of inner margin, 4 large subapical dorsal setae, 3 large apical dens, fine setae subapically (ventral surface), and 1 long seta near base (ventrally); stipes with 3 ventral setae, 1 very long; palpus 3-segmented; palpomere I long, narrowed apically; II smaller, cylindrical; III elongate, narrowed apically, with large dorsal seta near base, single lateral seta, subapical pore, and several apical sensillae (Fig. 9). Labium with 2 setae ventrally on prementum; mentum with 3 pairs of setae, 1 pair of pores; submentum reduced to narrow sclerotized band with 2 setae; palpus 2-segmented; palpomere I (width/length = 0.26) with mesal pore and 3 dorsal, distal setae; II (width/length = 0.25) with single ventral pore, 2 lateral pores, and about 7 apical sensillae (Fig. 10).

*Thorax* (Figs. 11, 12). Pronotum broad (length/width = 0.25), with large marginal setae (blunt, fimbriate-tipped); smaller, simple setae on disc; pore-like cuticular structures anteriorly; and 2 pairs of large, fimbriate setae on disc. Prosternum poorly defined, with 1 blunt seta and several smaller, simple setae; spiracle simple, circular, opening lined with minute setae. Metanotum similar to pronotum, with 3 pairs large, blunt setae on disc. Leg with large, elongate trochanter bearing ring of pores (including 2 dorsal and 5 ventral pores, 3 of which are arranged in transverse line) and several small, simple setae; femur stout, with long posterior seta near base, 3 dorsal setae, and about 8 ventral setae; tibia with 4 ventral setae (1 apico-lateral), 4 dorsal setae

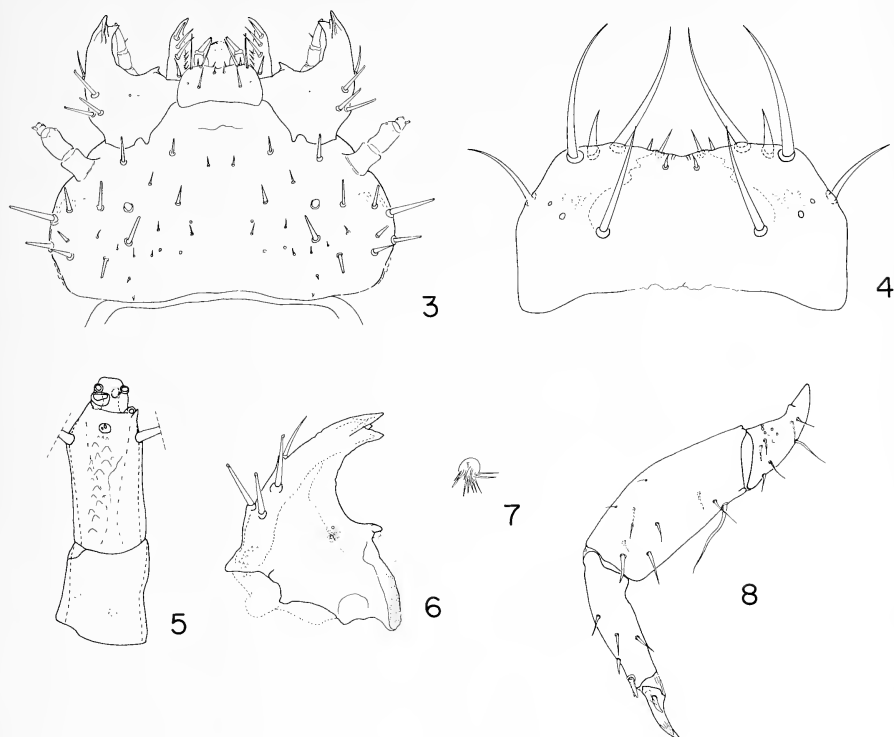


Figs. 1, 2. *Scotocryptus meliponae*, habitus, putative third-instar. 1. Dorsal view. 2. Lateral view.

(1 apicolateral); tarsungulus stout, surface minutely grooved, bisetose (setae short, stout) (Fig. 8).

**Abdomen.** Tergum I with 5 pairs large, blunt, dorsal setae; with smaller blunt setae in transverse line between larger setae (present between setae 2/3, 3/4, and 4/5); 1 large lateral seta near anterior angle; 1 large lateral seta near posterior angle; 1 large posterior seta near posterior angle; with smaller, simple setae and pores anteriorly (Fig. 13). Sternite I with 3 very long, simple setae and several smaller, simple setae. Other tergites and sternites similar in setal pattern. Tergite IX with long posterolateral setae; only a few simple, minute setae on disc; sternite with 3 long setae and several





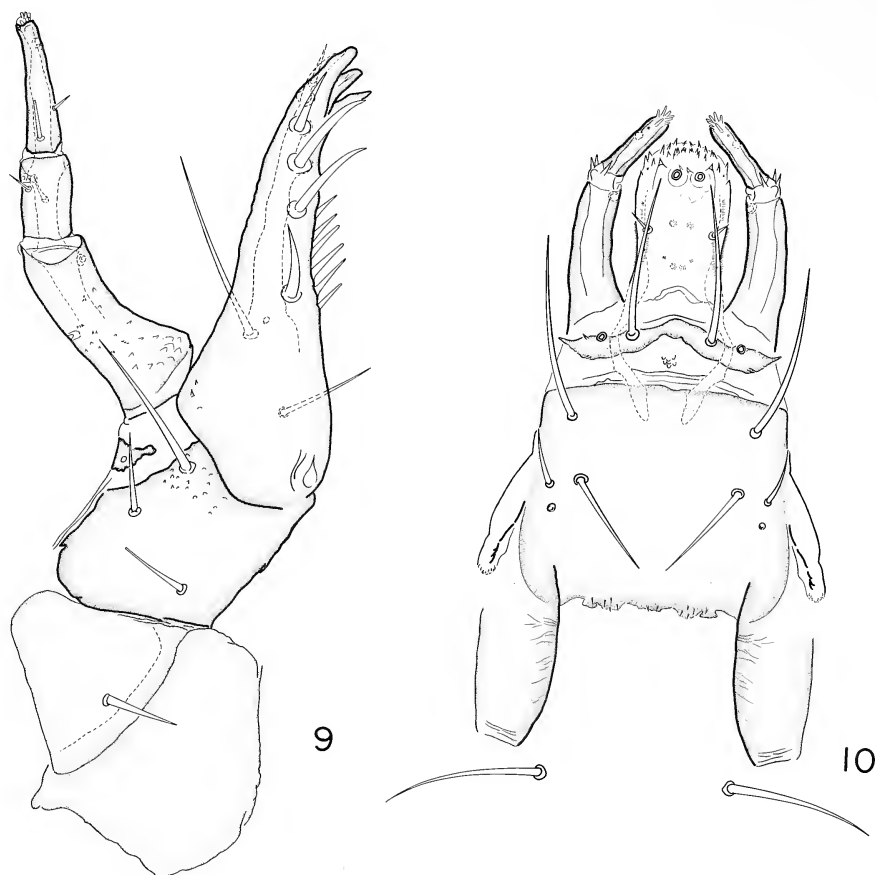
Figs. 3–8. *Scotocryptus meliponae*. 3. Cranium (dorsal). 4. Labrum (dorsal). 5. Antenna. 6. Left mandible (dorsal). 7. Mandibular sensillum (cf. Fig. 6). 8. Third leg (ventral).

smaller ones; urogomphus with stout base, bearing 1 large ventral seta, 2 large dorsal setae, several smaller setae, and terminating in very long, setose process.

#### ADAPTATIONS FOR INQUILINISM

Adult adaptations of *Scotocryptus* for inquilinism, including loss of flight and eyes, compact body form, grooves for appendages, and mandibular notches for grasping corbicular setae of hosts for phoretic flight, were presented by Salt (1929), Wilson (1971), and Roubik and Wheeler (1982). Larvae of these beetles, however, also exhibit apomorphs that appear to be adaptive for living in nests of meliponine bees. Stemmata are lost, paralleling blindness in adults. Dorsal setae are very heavy and while ostensibly tactile, they could be protective as well (Figs. 1, 2). Setae in related genera, such as *Creagrophorus* (Wheeler, 1979) and *Aglyptinus* (pers. obs.), are not so robust.

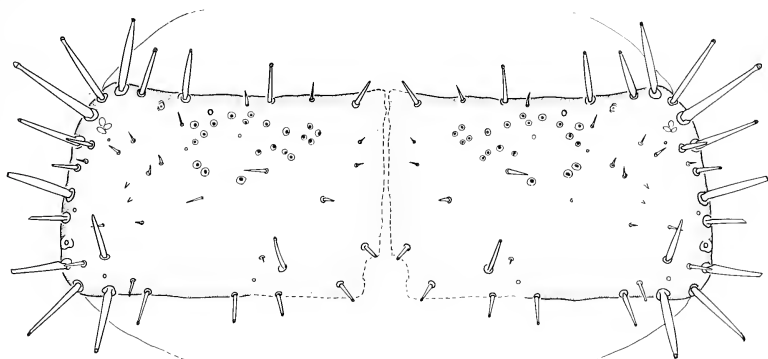
The pointed mala of the maxilla is distinctive from broader forms in related mycophagous leioidids, and is probably related to the ingestion of nest debris, largely consisting of bee feces (Roubik and Wheeler, 1982). Dorso-ventral compression of the body may also be a defensive adaptation, and there are porelike structures located



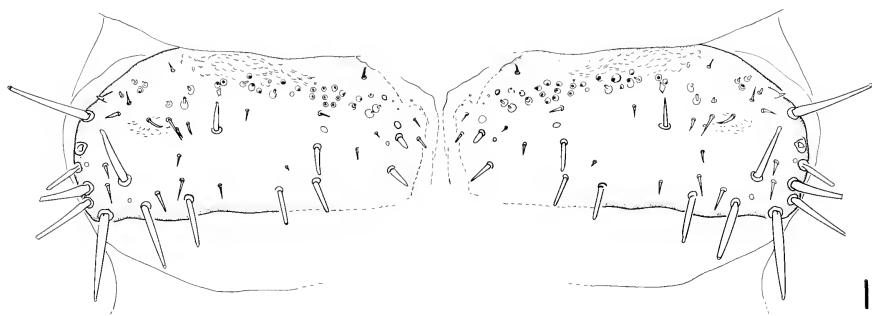
Figs. 9, 10. *Scotocryptus meliponae*. 9. Right maxilla (ventral). 10. Labium (ventral).

along the anterior margin of thoracic and abdominal terga of unknown function. Examination of these pores by compound microscopy reveals apparent cuticular openings, subtended by conical subcuticular areas. Even high magnifications (up to  $\times 1,000$ ), however, failed to find any evidence of cuticular reservoirs or ducts, associated with glands. Finally, the alcohol preserved specimens available to me were curved in an inverse c-shape. It is not known whether this posture is assumed by living beetles, but it is reminiscent of a defense posture reported by Arzone (1970, 1971) for a trufficolous species of *Leiodes*.

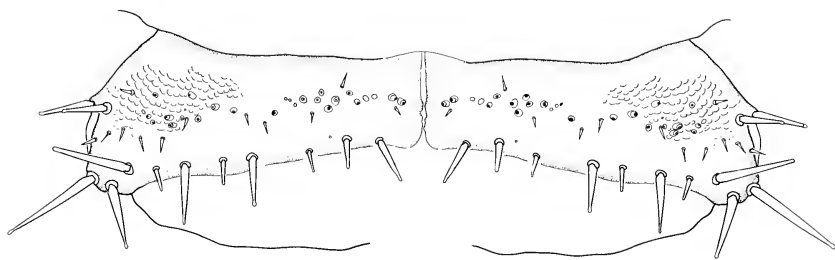
The adaptiveness of apomorphs is more easily speculated than demonstrated, and as Roubik and Wheeler (1982) suggested the larvae may be protected by neonatal acquisition of the nest odor, making the above speculations superfluous. Nonetheless, these structures are peculiar when compared to related, free-living beetles and the lives of scotocryptine larvae in the nests of their host bees deserve closer inspection.



11



12



13

Figs. 11–13. *Scotocryptus meliponae*. 11. Pronotum (dorsal). 12. Metanotum (dorsal). 13. Abdominal tergum I (dorsal).

## ACKNOWLEDGMENTS

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SPECIES STATUS AND THE HITHERTO UNRECOGNIZED MALE  
OF *PAPILIO DIAPHORA* STAUDINGER (1891),  
(LEPIDOPTERA: PAPILIONIDAE)

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*Abstract.*—*Papilio xanthopleura* var. *diaphora* is given species status based on examination of the holotype male and other specimens. Former usage applying *diaphora* only to a dimorphic aberration of the female is shown to be in error.

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For many years, *Papilio xanthopleura* var. *diaphora* Staudinger (1891) has been regarded as a dimorphic yellow aberration of the normally blackish female of *xanthopleura* Godman and Salvin (Rothschild and Jordan, 1906; Jordan 1907; Munroe, 1961; D'Almeida, 1965; D'Abrera, 1981). This traditional usage by lepidopterists appears to derive from Staudinger's (1891) concluding sentence in the description of *diaphora*: "so wird *Diaphora* nur eine dimorphe weibliche Form des *Xanthopleura*-♀ sein."

Recently, however, we discovered that a single "yellow female" identified as *xanthopleura* at the American Museum of Natural History (AMNH) was, in fact, a male. This led us to examine the morphology of this specimen in relation to the other taxa in the "scamander Group" of *Papilio* (*sensu* Jordan, 1906; Munroe, 1961; Hancock, 1983). Hancock (1983), in his phylogenetic classification of *Papilio sens. lat.*, which we will hereinafter follow, places this group in *Pterourus* (*Pyrrhosticta*). The "scamander Group," according to the above authors includes the taxa *scamander* Boisduval, *hellanichus* Hewitson, *birchalli* Hewitson, and *xanthopleura*. We obtained for comparison the type of *diaphora* from the Zoologisches Museum der Humboldt (ZMH) in Berlin, which also proved to be a male (see Fig. 1). We examined the text of Staudinger's "Neue exotische Lepidopteren" to ascertain the status of the name *diaphora*. We also sought to determine the known distribution of *xanthopleura* in South America from material in several of the world's major museums. This was necessary since *xanthopleura* and *birchalli* are noted by students and field collectors of *Papilio* as particularly rare, new specimens being available only in small numbers on the commercial butterfly market. Indeed, between the AMNH, Allyn Museum of Entomology (AME), British Museum (Natural History) (BMNH), Field Museum of Natural History (FMNH), and National Museum of Natural History (NMNH), only seventeen specimens of *xanthopleura* are known and none of these is a female. Prof. H. J. Hannemann (ZMH, pers. comm.) has acknowledged that the ZMH contains normal females of *xanthopleura* (as noted in Staudinger, 1891) and also another male specimen exhibiting the yellow morph characteristic of *diaphora*.

Examination of the AMNH male *diaphora* (Figs. 2, 3) and the type (Figs. 1, 3)



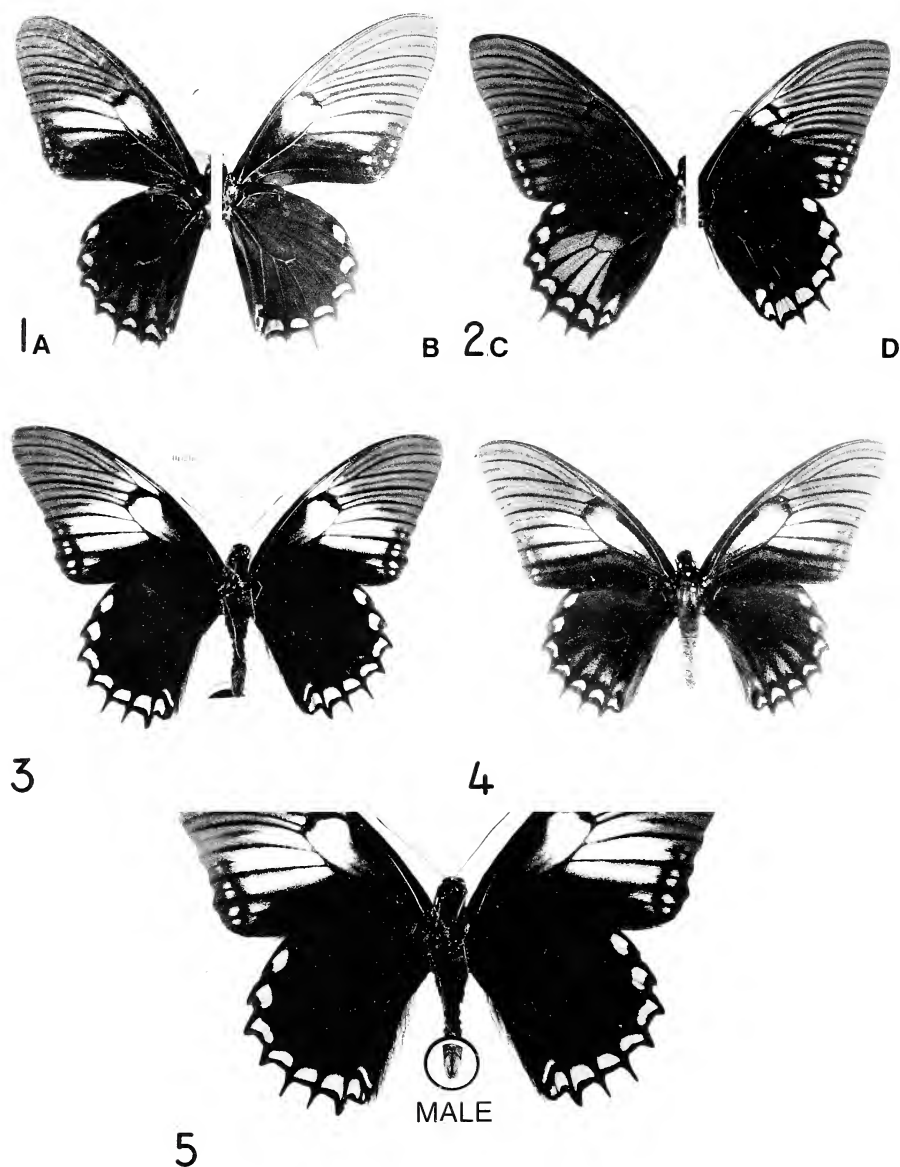


Fig. 1. *P. diaphora* (1, 3, 4, 5) and *P. xanthopleura* (2). 1, AMNH male *diaphora*: A, upper surface; B, under surface. 2, *xanthopleura*: C, upper surface; D, under surface. 3, Type of *diaphora* (ZMH): under surface. 4, Type of *diaphora*: upper surface. 5, Type of *diaphora* enlarged showing brushed abdominal terminus exposing male claspers.

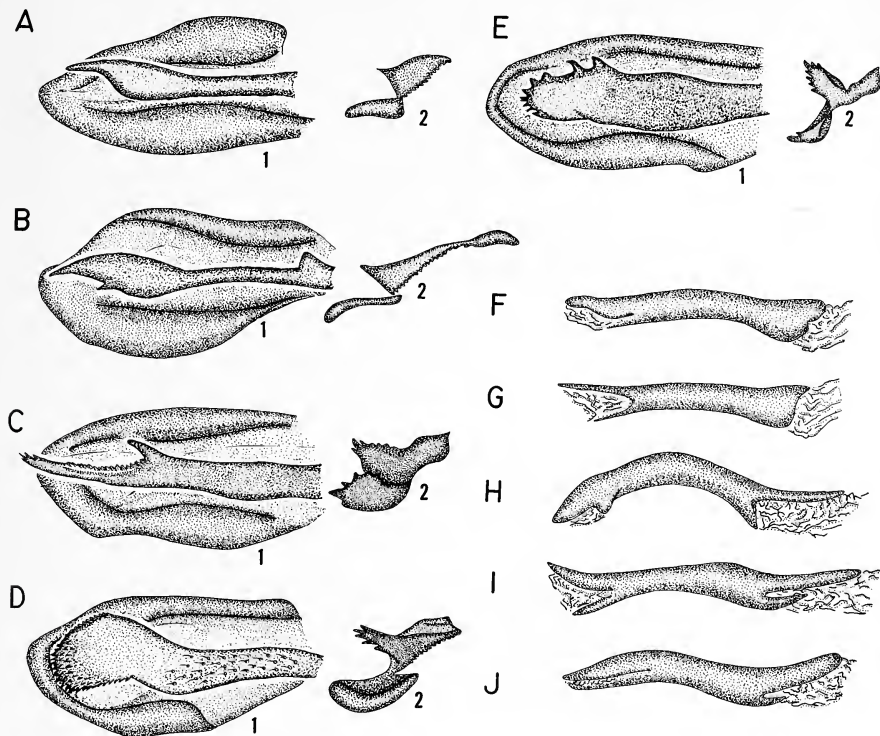


Fig. 2. Genitalia, the *scamander* Group. A, *scamander*: 1, inner lateral view of valve; 2, inner lateral view of socii. B, *hellanichus*: 1, 2, as above. C, *birchalli*: 1, 2, as above. D, *xanthopleura*: 1, 2, as above. E, *diaphora*: 1, 2, as above. Aedeagus F, *scamander*. G, *hellanichus*. H, *birchalli*. I, *xanthopleura*. J, *diaphora*.

indicates that along with the notable wing characters differentiating *diaphora* from *xanthopleura* and other taxa of the species group (Fig. 1), in the genitalia the valvular harpe of *diaphora* differs distinctly from all other taxa (Fig. 2). This is significant since students of the morphology of *Papilio sens. lat.* (Munroe, 1961; Hancock, 1983) utilize this character to differentiate amongst taxa of *Pterourus*. Notably, the harpe of *diaphora* (Fig. 2: E1) is like *birchalli* (Fig. 2: C1) in that both have terminal teeth pointing dorsad along an overall descending arch, whereas in *scamander*, *hellanichus*, and *xanthopleura* (Fig. 2: A, B, D, respectively) the arch is ascending with teeth variously apical and/or ventral. Differences are also apparent in the socii. Contrasted to *scamander* and *hellanichus* (Fig. 2: A2, B2, respectively), *xanthopleura*, *birchalli* and *diaphora* have generally hemispherical socii (Fig. 2: C2, D2, E2, respectively) but of these only *diaphora* and *birchalli* have furcations on the ventrad quadrasphere. The aedeagi (Fig. 2: F–J) of all the species are similar except *birchalli* in which it is notably curved. These characters clearly suggest that *diaphora* should be regarded as a species, part of a triad with *xanthopleura* and *birchalli*, and the sister species of

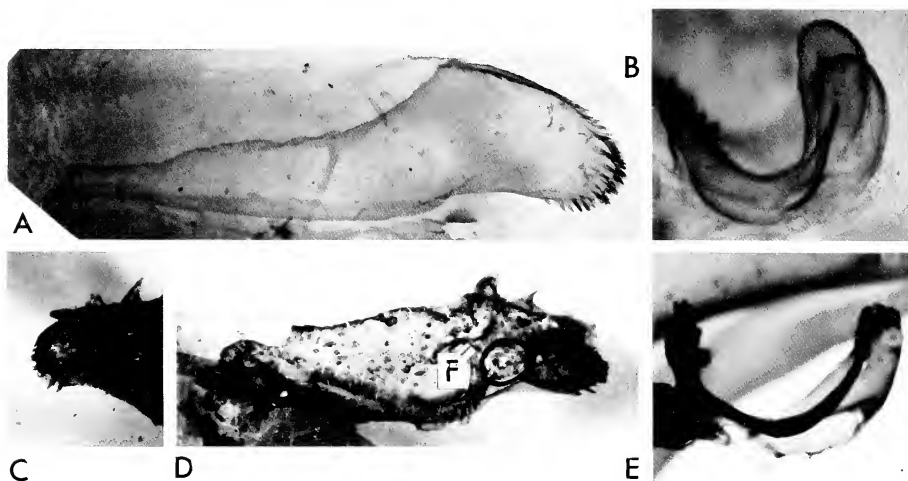


Fig. 3. Genitalia of *xanthopleura* and *diaphora*. A, *xanthopleura*: outer lateral view of valval harpe. B, *xanthopleura*: outer lateral view of socii. C, *diaphora*: outer lateral view of terminus of valval harpe not figured in Figure 2. D, *diaphora*: outer lateral view of valval harpe figured in Figure 2 with F, location of a lateral spine (on inner surface) not present in *xanthopleura*. E, *diaphora*: outer lateral view of right socii. *P. diaphora* photos from AMNH male; *xanthopleura* from Uaupes, Brazil, AMNH.

*xanthopleura*. *P. diaphora* is most like *xanthopleura* in the wings, but in the genitalia displays notable resemblances to *birchalli*.

Study of the original description in "Neue exotische Lepidopteren" indicates that the limitation of *diaphora* to a morph of the female can be judged in error. Throughout his text, Staudinger used the categories "variety" ("var. xus") and "aberration" ("ab. xus") consistently, and when in doubt "var. (ab.?) xus." In the description of *diaphora* Staudinger entertained that it may be a "consistent local form," "dimorphic female form" or, perhaps a valid species. Further, the initial citation of *diaphora* (Staudinger, 1891, p. 63) was as a trinomen, whereas elsewhere in his text Staudinger also used quadrinomials. Hence, according to our reading of ICZN Article 45, sections (d) (i), (iii), and (e) (i), the name *diaphora* can be judged as available.

*Pterourus (Pyrrhosticta) diaphora* (Staudinger),  
New Combination, Revised Status

*Papilio xanthopleura* Godman and Salvin var. *diaphora* Staudinger, 1891, p. 63.

*Papilio xanthopleura* Godman and Salvin ♀ var. *diaphora*: Rothschild and Jordan, 1906, p. 633.

*Papilio xanthopleura* ♀ f. *diaphora*: Rothschild and Jordan, 1906, p. 633. Jordan, 1907, p. 32. D'Almeida, 1965, p. 278.

*Papilio xanthopleura* ♀ form [*diaphora*]: D'Abrera, 1981, p. 50.

*Male*. Compared to all taxa of *scamander* Group, wings most like *xanthopleura* (in that both lack the broad yellow bands across both wing upper surfaces charac-

teristic of *hellanichus* and *scamander*) and thereafter *birchalli* (which has a broad yellow band limited to the hindwing upper surface only). Wings differing from *xanthopleura* as follows: (1) forewing at least one-sixth longer than *xanthopleura*; (2) upper surface of forewing not completely dark as in *xanthopleura* but with bright yellow patch from central area of discal cell distad to postmedian areas from vein  $M_2$  to  $CU_2$  and with powdered yellow over most of subapical area; (3) upper surface of hindwing not generally shiny "powder green" from median area distad as in *xanthopleura* but deeply iridescent navy blue throughout with only small "powder green" chevrons in the vein interspaces along the margin; (4) tail at terminus of vein  $M_3$  notably longer than others, not with tails of approximately equal length as in *xanthopleura*; (5) under surface similar to *xanthopleura* except (a) *diaphora* with bright yellow patch expansive on forewing across entire median and postmedian area from center of discal cell to the outer margin and (b) *diaphora* with hindwing marginal orange chevrons only becoming yellow at the anal angle in a slightly hemispherical patch, not in two large yellow chevrons at anal angle and basad in cell 2V as in *xanthopleura*. Length of forewing: AMNH, 67.5 mm; ZMH (type), 71.0 mm.

*Female*. Unknown (but see Rothschild and Jordan, 1906).

*Male genitalia*. Figures 1, 2, 3. Valval harpe (1: 5; 2: E1; 3: C, D, F) with marked dorsad teeth along generally descending terminal arch. Socii (2: E2; 3: E) hemispherical with ventrad quadrasphere furcate. Aedeagus (2: J) not radically curvate.

*Female genitalia*. Unknown.

*Holotype*. ♂ BRAZIL: Amazonas: Manicoré, deposited ZMH bearing labels "Origin," "Papilio xanthopleura var. diaphora Stgr., " "Manicoré, Rio Madeira, 1887, Hahnel," "Zool. Mus. Berlin."

*Distribution*. Spatial: Figure 4. Indicated as sympatric with *xanthopleura* as follows.

**P. diaphora**: BRAZIL: Manicoré (ZMH, type); São Paulo de Olivença (Michael, pers. comm., Rothschild and Jordan); BRAZIL/BOLIVIA: Between Porto Velho, Brazil, and Villa Bella, Bolivia (AMNH).

**P. xanthopleura**: BOLIVIA: Bolivia (BMNH). BRAZIL: Campana (AMNH); Cuiabá River (BMNH); Madeira River (NMNH); Manicoré (Staudinger); São Paulo de Olivença (Staudinger, Rothschild and Jordan); São Thomás (Staudinger, Rothschild and Jordan); Rio Negro (Rothschild and Jordan); Uaupes (AMNH); Upper Amazon (BMNH). ECUADOR: Napo River (BMNH). PERU: Eastern Peru (Staudinger); Iquitos (AME, BMNH, NMNG, Staudinger, Rothschild and Jordan); Peru (Rothschild and Jordan); Pichis (Matusik); Rio Huallaga (Rothschild and Jordan).

#### DISCUSSION

Four specimens of *diaphora* are evidenced: the type, the AMNH male, a male subsequently reported in the ZMH (Hannemann, pers. comm.), and a reputed female reported pers. comm. by Michael (Rothschild and Jordan, 1906). Additional data on the AMNH male is found on accession card No. 3955, Registrar's Acc. No. 15861, date received January 10, 1912, from D. P. Davis, Marlborough Hotel, New York City, New York, from locality "Between Porto Velho, Brazil, and Villa Bella, Bolivia." Card has been placed with AMNH specimen.

Our diagnosis (Fig. 1) of the type of *diaphora* as a male suggests the female of *diaphora* may be unknown, depending on the veracity of Michael's identification



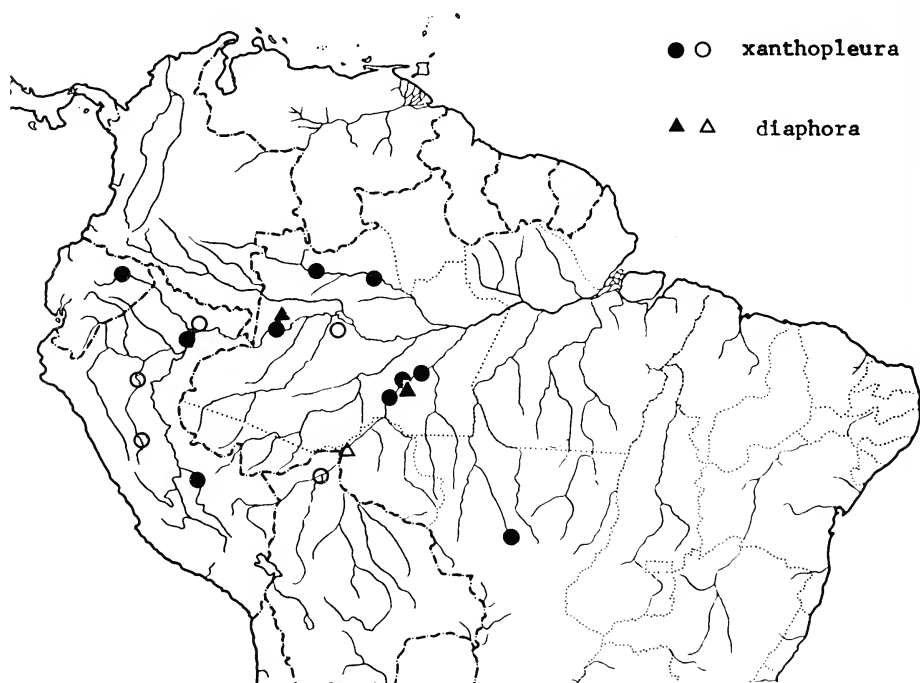


Fig. 4. Geographic distributions of *P. xanthopleura* (●, exact data; ○, generalized locality data) and *P. diaphora* (▲, exact data; △, generalized locality data).

(Rothschild and Jordan, 1906). The misdiagnosis of the type gender of *diaphora* has contributed to the view of *diaphora* as an aberration of the female of *xanthopleura*. The following factors probably contributed to this misdiagnosis: (1) the abdomen of the type was profusely hairy and upon ventral examination exhibited a small opening with protruding spines suggesting papillae anales. The lateral area of the abdomen, however, clearly suggested claspers to us and our subsequent examination of the genitalium confirmed this; (2) the large size of *diaphora* (all *xanthopleura* seen by us in this study have been under 60 mm); (3) female variation in some superficially similar groups of *Papilio* (like widely variant *Papilio androgeus* Cramer) includes a frequency of large yellow-patched females contrasting the more common and smaller dark-winged females. The assumption that large yellow-patched specimens were females may have contributed to the lack of reference to the genitalia of *diaphora* hitherto. We dissected the type of *diaphora* and this dissection corroborates the characters of *diaphora* in the AMNH male. We are returning this dissection in permanent mount to the ZMH and retaining photographs at the AMNH.

#### ACKNOWLEDGMENTS

We are particularly grateful to Prof. H. J. Hannemann (ZMH) for providing the type of *diaphora* for examination. Four anonymous reviewers made helpful comments, particularly



concerning the type depository and the status of *diaphora*. In addition, Drs. Frederick H. Rindge, Randall T. Schuh, Lee H. Herman (AMNH), Klaus Sattler (BMNH), Lee D. Miller (AME), and G. Bernardi (Museum National d'Histoire Naturelle, Paris) gave opinions concerning the latter. Not all agreed, however, with the decision that *diaphora* was available. The above persons, along with Mr. Richard Vane-Wright and Mr. Philip Ackery (BMNH) and Dr. Robert K. Robbins (NMNH) variously aided in the securing of distributional data for *xanthopleura*. Eric Quinter (AMNH) aided in the study of the type of *diaphora*. Bonnie T. Gardner provided the drawings from permanent mounts at the AMNH.

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## REVISION OF THE NEARCTIC SPECIES OF *HYSSOPUS* GIRAULT (HYMENOPTERA: EULOPHIDAE)

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*Abstract.*—The Nearctic species of *Hyssopus* Girault (Hymenoptera: Eulophidae) are revised for the first time. Eight species are included and lectotypes are designated for *novus* Girault and *benefactor* (Crawford). A key to the species is presented. Two new taxa (*clypealis*, and *aaba*) are described and illustrated and several new host records are listed. All species of *Hyssopus* are primary parasites of lepidopterous larvae that mine or bore in twigs, cones, and stems.

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Girault (1916) proposed the generic name *Hyssopus* for a single species, *thymus*. Since that time, several other species have been described from North America by other authors (e.g., Gahan, 1927), and other species have been transferred to *Hyssopus* from related genera. However, the included species have never been revised, and there has been considerable difference of opinion over the limits of the genus. Boucek (1965) stated that the species were at best a subgenus of *Elachertus*. Askew (1964) also recognized that these species formed a distinct group but kept them in *Elachertus*. More recently, authors (e.g., Burks, 1979; Graham, 1983; Boucek, pers. comm.) have treated *Hyssopus* as a valid genus separate from *Elachertus*.

The species of this genus are all primary parasites of the larvae of Lepidoptera that mine or bore in the stems, twigs, or cones of various trees and shrubs. Some of these are major pests of forest trees (e.g., *Rhyacionia frustrana* (Comstock), the Nantucket Pine Tip Moth) or ornamentals (e.g., *Synanthedon scitula* (Harr.), the Dogwood Borer).

All types, including new species, are deposited in the U.S. National Museum of Natural History. Many of the older types are in poor shape, having been poorly mounted originally or subsequently mishandled. The heads of most of the species were removed by Girault and mounted on slides. Unfortunately, several of them were smashed, and the fragments make it extremely difficult or impossible to see certain features of the ocelli, vertex, and so on. This problem has been circumvented in some species by the naming of intact specimens from the syntype series as lectotype. However, in those cases where a holotype was designated or only a single specimen was described, this has not been possible, and the inability to see certain features on the head of these specimens has been a problem during the course of this study.

Names of hosts follow Hodges et al. (1983). Common names of hosts are from Werner (1982). New host and locality records established during the course of this study are marked by “\*.” Nomenclature for sculpturing follows Harris (1979). Head height, width, and eye height is measured in frontal view and at the widest point. Eye width is measured in lateral view. All measurements and ratios were taken with

an eyepiece reticle. Abbreviations for museums are given in the acknowledgments. The key to species will work for both males and females, there being little in the way of sexual dimorphism in this genus.

#### KEY TO SPECIES

1. Head in front view as high or higher than wide (Figs. 1, 2); gaster covered posteriorly and laterally with imbricate sculpturing (Fig. 11); median propodeal carina weakly expressed, barely raised from the surface, and occasionally nearly absent (Fig. 6); hindfemora swollen medially, less than  $3\times$  as long as wide ..... 2
- Head in front view wider than high (Figs. 3, 4); gaster smooth; median propodeal carina strongly expressed, complete and raised from the surface (Figs. 7, 8); hindfemora cylindrical, more than  $3\times$  as long as wide ..... 4
2. Head in front view as high as wide (Fig. 1); eye height less than  $\frac{1}{2}$  head height; scutellum about as long as wide; hindfemora about  $2\times$  as long as wide ..... *rhyacioniae* Gahan
- Head in front view higher than wide; eye height more than  $\frac{1}{2}$  head height (Fig. 2); scutellum longer than wide; hindfemora about  $3\times$  as long as wide ..... *novus* Girault
3. Vertex covered by erect black setae; eyes with numerous silvery setae (Fig. 4); side lobes of scutum with 2 enlarged setae at medial margin (Fig. 10); uncus with 5 sensillae (Fig. 17) ..... *aaba*, new species
- Vertex covered by small, usually silver or white setae; eyes bare or with few scattered and inconspicuous setae (Fig. 2); side lobes of scutum with single large seta at medial margin; uncus with 4 sensillae ..... 5
4. Clypeus produced forward from margin of oral cavity (Fig. 14); mandibles and all coxae yellow ..... *clypealis*, new species
- Clypeus not produced forward from margin of oral cavity (Fig. 15); at least one pair of coxae or mandibles brown or black ..... 6
5. Scutellum and axillae smooth (Fig. 9); dorsum usually flat, metanotum and propodeum on about same plane as scutellum ..... *johannseni* (Crawford)
- Scutellum and axillae covered by light alutaceous sculpture (Fig. 7); dorsum usually inclined, metanotum and propodeum sloping away from plane of scutellum ..... 7
6. Hind margin of compound eye in dorsal view reaching posterior margin of head (Fig. 18); mandibles with five teeth ..... *benefactor* (Crawford)
- Hind margin of compound eye in dorsal view not reaching posterior margin of head (Fig. 19); mandibles with 6 teeth (Fig. 16) ..... 8
7. Propodeal carina flaired and raised anteriorly (Fig. 8); metanotum barely expanded medially, petiole as long as wide ..... *sanninoideae* (Girault)
- Propodeal carina not raised anteriorly (Fig. 7); metanotum distinctly triangular, petiole wider than long ..... *thymus* Girault

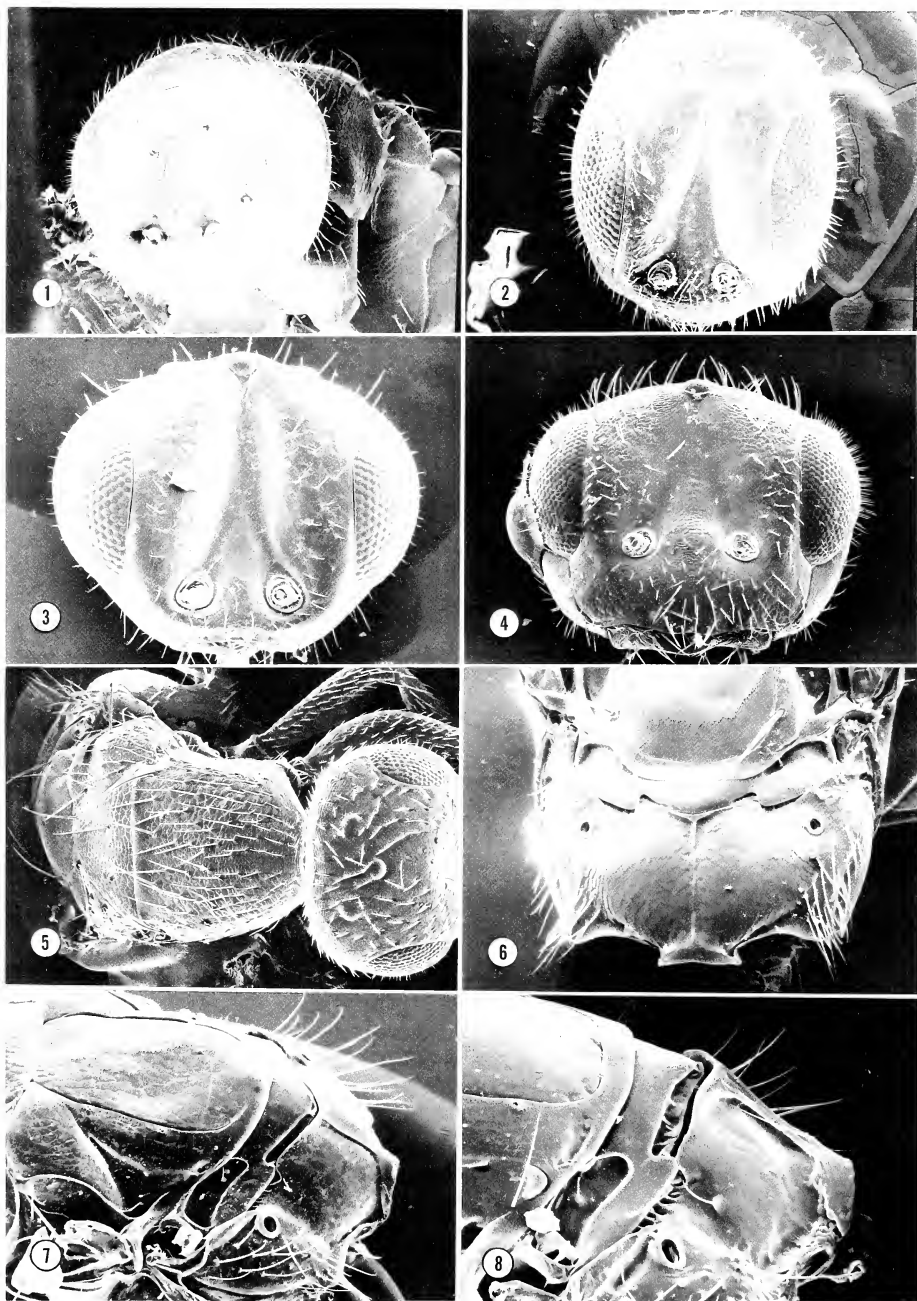
#### Genus *Hyssopus* Girault

*Hyssopus* Girault, 1916:115. Type species: *Hyssopus thymus* Girault. Monotypic.

*Hyssopiscus* Ghesquière, 1946:370. Unnec. new name.

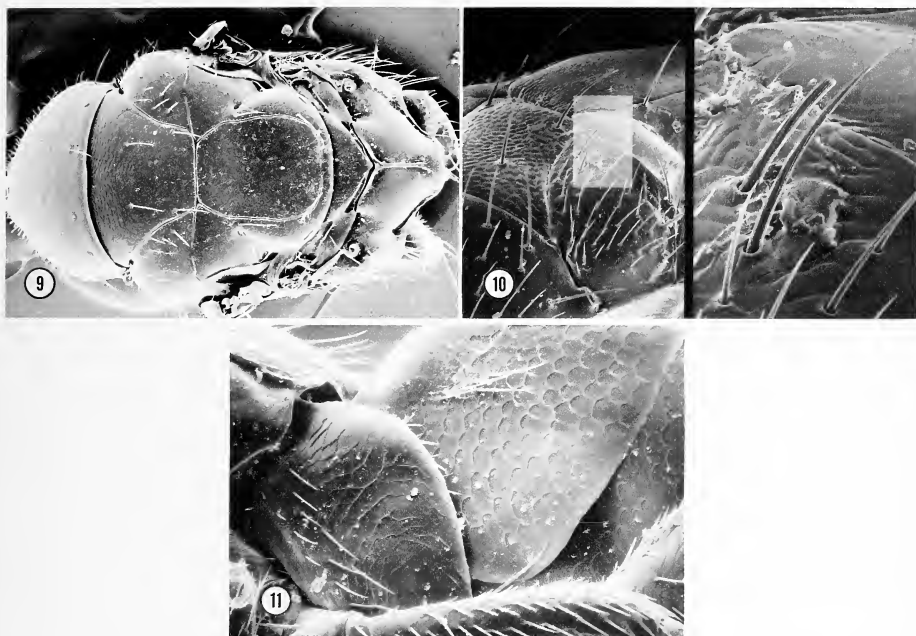
*Crataepoides* Masi, in Zinna 1955:66. Type species: *Crataepoides russoi* Zinna. Orig. desig.

*Diagnosis.* Postmarginal and stigmal veins well developed; funicle 4-segmented, club 2-segmented (Figs. 12, 13); scutellum with a pair of parallel lateral grooves curving inwards posteriorly (Figs. 6, 9); pronotum as long as wide, about as wide as scutum (Fig. 5), sloping gradually toward the foramen, and not abruptly narrowed



Figs. 1-8. 1-4. Heads of *Hyssopus* spp. 1. *H. rhyacioniae*. 2. *H. novus*. 3. *H. thymus*. 4. *H. aaba*. 5. Dorsal pronotum and head of *H. rhyacioniae*. 6. Propodeum of *H. novus*. 7. Scutellum and propodeum of *H. thymus*. 8. Lateral propodeum of *H. sanninoideae*.



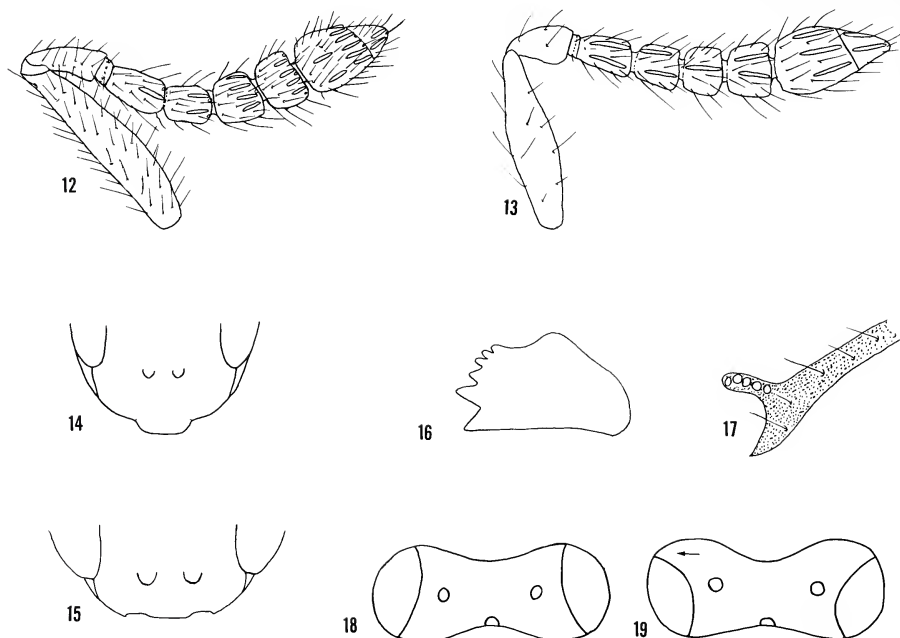


Figs. 9–11. Dorsal thorax of *H. johannseni*. 10. Lateral scutum of *H. aaba*. 11. Hindcoxa and lateral gaster of *H. novus*.

anteriorly; covered with coriaceous sculpturing; mid lobe of scutum with four setae (Fig. 9), notauli meeting scutellum near inner angles of axillae; body generally black or dark reddish brown.

*Discussion.* This genus is very closely related to *Elachertus* Spinola, as mentioned above. Unfortunately, *Elachertus* is also in need of revision, and the limits of that genus have not been rigorously defined. The North American species of *Elachertus* do share a similar habitus, but until those species have been revised it remains a possibility that the characters used to distinguish the group are plesiomorphic. Nevertheless, for the purposes of character polarity, *Elachertus* as currently defined is the most likely sister taxon of *Hyssopus*. From my study of *Elachertus* and related genera, I believe that *Hyssopus* can be defined by the following shared derived states: pronotum in dorsal view about as long as wide or longer, sloping gradually toward the foramen, about as wide as the scutum, and not narrowed anteriorly; midlobe of scutum with only four setae. In related groups, the pronotum in dorsal view is usually distinctly wider than long, narrows anteriorly, and slopes abruptly, sometimes almost vertically, towards the foramen. The possession of four scutal setae is more problematic, since it occurs in other more distantly related genera. However, in *Elachertus* and other closely related genera the scutum is generally covered by at least 6 setae and occasionally many more. Therefore, I believe that the condition seen in species of *Hyssopus* is synapomorphic for that group.





Figs. 12-19. 12, 13. Antennae. 12. *H. aaba*. 13. *H. clypealis*. 14, 15. Frontal views of head. 14. *H. clypealis*. 15. *H. sanninoideae*. 16. Mandible of *H. thymus*. 17. Stigmal vein and uncus of *H. aaba*. 18, 19. Dorsal view of heads. 18. *H. benefactor*. 19. *H. thymus*.

### *Hyssopus novus* Girault

*Hyssopus novus* Girault, 1917b:3.

**Diagnosis.** Femora swollen medially, less than  $3\times$  as long as wide; head in front view higher than wide; eye height more than  $\frac{1}{2}$  head height (Fig. 2); gaster covered posteriorly and laterally by imbricate sculpturing (Fig. 11); scutellum longer than wide; median propodeal carina weak (Fig. 6); hindtibia dark brown or black.

This species is most closely related to *rhyacioniae*. It can be separated by the following: head as high as wide (higher than wide in *rhyacioniae*), eye height more than  $\frac{1}{2}$  head height (less than  $\frac{1}{2}$  head height in *rhyacioniae*), and the scutellum as long as wide (longer than wide in *rhyacioniae*).

**Hosts.** Pyralidae: *Dioryctria ponderosae* (Dyar)\*, *D. auranticella* (Grote)\*; *D. cambiicola* Dyar\*. Tortricidae: *Rhyacionia neomexicana* (Dyar)\*.

**Distribution.** Calif., Idaho\*, N.M.\*, Ariz.\*, Colo.\*

**Types.** Girault did not specify how many specimens he saw when he described this species, but the USNM type records indicate that there were only two. The lectotype female (present designation) is point mounted with the following data: Hopkins U.S. no. 14265, reared, *Pinus attenuata*, parasite of *Dioryctria xanthaenobares*, Patricks creek, California, J. M. Miller collector, Sept. 15, 1916. USNM type no. 21376. Paralectotype female with same data.

The lectotype is nearly intact, except for the antennae (lower right coverslip) which were mounted on the same slide as the head, antennae, and parts of the legs of the paralectotype. This slide is labelled with the species name and the type number in Girault's hand. The paralectotype is also missing its pronotum and one set of wings.

*Other specimens examined.* 39 females and 2 males (USNM).

*Variation.* Size ranges from from 1.6 to 1.8 mm. Color is generally dark reddish brown to black. The scape, flagellum, and legs vary from light brown or yellowish to black, usually with the distal tips of the femora and tibiae lighter than the rest of the leg. The base of the gaster on some specimens is distinctly lighter in color than the rest of the gaster. Sculpturing of the scutellum and area laterad of the median propodeal carina varies from nearly smooth to distinctly alutaceous. The median propodeal carina is generally complete in this species, but is slightly more weakly expressed in some specimens. The eyes of some specimens appear to be distinctly setose, as mentioned by Gahan in his description of *rhyacioniae*. However, I do not find that it is a reliable difference, since some of the specimens of *novus* have eyes whose setation appears nearly indistinguishable from those of *rhyacioniae*.

*Hyssopus rhyacioniae* Gahan

*Hyssopus rhyacioniae* Gahan, 1927:546.

*Diagnosis.* Femora swollen medially, less than  $3\times$  as long as wide; head in front view as wide as high; eye height less than  $\frac{1}{2}$  head height (Fig. 1); scutellum about as long as wide; gaster covered posteriorly and laterally by imbricate sculpturing (Fig. 11); hindfemora about  $2\times$  as long as wide; hindtibiae light brown or yellow.

This species is most closely related to *novus* Girault. It may be separated by the following: head as high as wide (higher than wide in *novus*), eye height less than  $\frac{1}{2}$  head height (more than  $\frac{1}{2}$  head height in *novus*) and scutellum as long as wide (longer than wide in *novus*).

*Hosts.* Pyralidae: *Dioryctria abietivorella* (Grote), *D. amatella* (Hulst) (Southern Pine Coneworm), *D. cambiicola* (Dyar), *D. zimmermani* (Grote) (Zimmerman Pine Moth). Tortricidae: *Rhyacionia frustrana* (Comstock) (Nantucket Pine Tip Moth). Sesiidae: *Synanthedon pini* (Kellicott)\*. The original label on this series of specimens indicates that the series was reared from *Parharmonia pini*. *Parharmonia* is now considered a synonym of *Albuna* Henry Edwards. Unfortunately, there is no species *pini* currently assigned to that genus. The closely related genus *Synanthedon* Hubner (from which other species of *Hyssopus* have been reared) does contain a species *pini* (Kellicott) and it is likely that this is the species referred to by the label (D. Weissman, pers. comm.).

*Distribution.* N.Y., Virg., Md., S.C., Ga., Miss., Ark., La., Fla., Ill., Ind., Wisc., Ohio, Tex., and Ontario. Since Burks' summary of distribution did not list individual states, it is not possible to say if some of the state records listed above may be new.

*Types.* Holotype female on point with data: Virginia, E. Falls Church. 6-25-1916. R. A. Cushman collector. Ex. *Rhyacionia frustrana* (Comst). USNM type no. 40179. Two male and 15 female paratypes with same data as holotype, except dates range from 6-25 to 7-11.

*Other specimens examined.* 12 females and 1 male (CNC), 80 females and 2 males (USNM).

*Variation.* Length varies from 1.3 to 1.8 mm. Body color ranges from reddish brown to black. The scape, pedicel, parts of the funicle, femora, and tibiae vary in color from light brown or yellowish to black. The base of the gaster is occasionally somewhat lighter in color than the rest of the gaster. The median propodeal carina is nearly absent in some specimens. The paratype males (reared from *Rhyacionia*) are quite similar to the females. However, three male specimens (two of which were reared from *Dioryctria amatella* along with females of this species) are quite different when compared to the males from the type species. The males from *Dioryctria* have an enlarged head ( $1\frac{3}{4}$  to  $2\times$  as wide as the pronotum), reduced eyes, increased numbers of setae on the frons and vertex, the scape is swollen apically, the mandibles are enlarged, and the femora are broader than in normal males and females. I believe that this morphological difference may be related to host, but additional rearings would be needed for a definitive answer. A single series of three specimens reared from *Synanthedon pini* (see above) have the teeth of the mandibles blunted.

*Hyssopus thymus* Girault

*Hyssopus thymus* Girault, 1916:115.

*Diagnosis.* Head in front view wider than high; gaster smooth; hindfemora cylindrical, more than  $3\times$  as long as wide; propodeal carina complete, well developed (Fig. 7); scutellum and axillae alutaceous; head in dorsal view with compound eye not reaching posterior margin of occiput (Fig. 19); mandibles with 6 teeth.

This species is most closely related to *sanninoideae* (Girault) and *benefactor* (Crawford), all of which have the scutellum covered by light alutaceous sculpturing. However, *sanninoideae* has the median propodeal carina distinctly raised and flaired anteriorly (carina only slightly raised and not flaired anteriorly in *thymus*) and the petiole is as long as wide (petiole a narrow band, not longer than wide in *thymus*) and *benefactor* has the posterior margin of the compound eyes contiguous with the hind margin of the head (Fig. 18) (posterior margin of eyes not reaching back of head in *thymus*, Fig. 19) and the mandibles with 5 teeth (mandibles with 6 teeth in *thymus*). It is also very similar to *johannseni* (see discussion under that species) but can be separated by the sculpturing of the scutellum (smooth in *johannseni* and alutaceous in *thymus*).

*Hosts.* Pyralidae: *Dioryctria auranticella* (Grote), *D. zimmermani* (Grote) (Zimmerman Pine Moth). Tortricidae: *Petrova comstockiana* (Fern.) (Pitch Twig Moth), *P. wenzeli* (Kft.), *Rhyacionia buoliana* (D. & S.) (European Pine Shoot Moth), *R. frustrana* (Comstock) (Nantucket Pine Tip Moth), *R. rigidana* (Fern.) (Pitch Pine Tip Moth), *Endothenia albolineana* (Kft.)\* (Spruce Needleminer). Gracillariidae: *Marmara* sp.\* Gelechiidae: *Metzneria lappella* (L.)\*. Coleophoridae: *Coleophora cratipennella* (Clem.)\*, *C. concolorella* (Clem.)\*.

*Distribution.* N.H.\*, Vt.\*, N.Y., Conn., Ohio, Virg., Mich., Ill., Wisc., N.D., Calif., Tex., Fla., Ontario, Sask.\*, Que.\* Peck (1963) also cites a record from Nebraska.

*Types.* Holotype female on point with data: Nebraska, Lincoln. G. I. Rewes collector. Webster no. 2142. USNM type no. 19922. Girault mounted the head, antennae, one forewing, and two legs of the type. This slide is labelled with the species name and the above type no. The head is badly crushed and the antennae are disarticulated. The other wings have apparently been lost.

*Other specimens examined.* 118 females, 17 males (CNC); 2 males, 1 female (SWE); 49 females, 2 males (DCD); 151 females, 14 males (USNM), 1 female (INHS).

*Variation.* Length varies from 1.0 to 2.5 mm. Body color is generally black, with some smaller specimens tending to be light brown or reddish. The coxae are almost always black except in smaller specimens in which they may be brownish yellow. Likewise, the femora and occasionally the tibiae and tarsi are black or dark brown but may become lighter colored in smaller specimens. In critical point dried specimens, the gaster is usually light brown with the base slightly lighter colored than the rest and the ovipositor sheaths may reach slightly past the tip. Air dried specimens, in which the gaster has collapsed generally do not have the ovipositor sheaths reaching much past the tip of the gaster. The scutellum sculpturing varies from distinctly alutaceous to nearly smooth, but there is always at least some sculpturing anteriorly.

*Hyssopus johannseni* (Crawford)

*Elachertus johannseni* Crawford, 1912:181.

*Elachistus evetriae* Girault, 1917a:1. New **Synonymy.**

*Diagnosis.* Head in front view wider than high; gaster smooth; hindfemora cylindrical, more than  $3 \times$  as long as wide; propodeal carina complete, well developed (as in Fig. 7); scutellum and axillae smooth; metanotum and propodeum on about same plane as scutellum.

This species is closely related to *sanninoideae* and *thymus* from which it differs mainly in having the scutellum and axillae smooth (scutellum and axillae sculptured in other species). In addition, the dorsum of the thorax is generally quite flattened in specimens of *johannseni*, with the scutellum, metanotum and propodeum all on the same plane. In the other species the metanotum and propodeum slope to some extent away from the plane of the scutellum.

*Hosts.* Tortricidae: *Barbara colfaxiana taxifoliella* (Busck.); *Mellisopus latiferreanus* (Wlsm.); *Petrova albicapitana* (Busck.) (Northern Pitch Twig Moth); *P. wenzeli* (Kearf.); *Cydia* sp. (previously *Laspeyresia* sp.); ? *Endothenia montanana* Kearf.\* (see following). A series of specimens from Manitoba (loaned from CNC) bears the host name "*Thiodia montanata* Kearf." However, I can find no reference to such a combination. There is, however, a species *Endothenia montanana* Kearfott, which is almost certainly the species referred to on the label of these specimens.

*Distribution.* Maine, Virg., Miss., Colo.\*, Utah\*, Ore., Alberta\*, Manitoba\*. Burks (1979) also lists Minnesota and Idaho as localities for this species, records which he probably established from his identification work. In addition, Peck (1963) cites a record from Ohio. However, I have not seen specimens from these areas and cannot confirm them.

*Types.* Holotype female of *johannseni* on point with data: Orono, Maine. July, 1911. Maine experiment station Lot 1386, sub 5. USNM type no. 14595. Head, antenna, and parts of legs on slide. The type specimen is in very poor shape. Girault slide mounted the head, antennae, and parts of the legs and the head is badly crushed. The remainder of the specimen was apparently originally mounted on a minuten pushed through the gaster. The gaster remains on the minuten, but the thorax is now attached in a large spot of glue to the surface of the block holding the minuten and much of the thorax is obscured.

Although Girault did not specify how many specimens he saw when he described *evetriae*, there are 3 specimens labelled as types in the USNM collection and the type records indicate that there were only 3 specimens in the original series. The types of *evetriae* are largely intact, except for one specimen which has the head slide mounted and crushed.

*Other specimens examined.* 109 females, 17 males (USNM); 46 females, 15 males (CNC).

*Variation.* Size varies from 1.6 to 2.5 mm. Color of the legs varies somewhat, with the femora and particularly the tibiae fading from black to brown or yellowish in some specimens. The base of the gaster in some males is brownish. The scutellum and axillae are usually slightly advanced beyond the posterior margin of the scutum, but in a few specimens they end in a straight line with it. The scutellum is generally distinctly longer than wide, but in a few smaller specimens it becomes somewhat expanded laterally and nearly as wide as long. Finally, some specimens have the sculpturing of the scutum and posterior margin of the pronotum faded from the normal alutaceous to nearly smooth.

*Discussion.* *H. evertriae* was described by Girault from material collected in Oregon, and *johannseni* was described from material collected in Maine. Although the two species were kept separate by later authors largely on the basis of their distribution, specimens are now available from intermediate localities. I find no morphological differences to indicate that they are not the same species and propose the above new synonymy. A similar problem exists between this species and *thymus* Girault. There is a distinct difference between the types and the majority of the reared series of the two species as indicated by the differences presented in the key and diagnoses. However, after studying several series of specimens there appear to be some specimens that are intermediate between the two different morphological types. In addition, the ranges of the two species overlap, and the hosts are similar although not identical. Finally, the scapes of the males of both species tend to be somewhat swollen medially. Nonetheless, at this time, the amount of material is limited, and I am reluctant to synonymize the two species without additional reared specimens.

*Hyssopus benefactor* (Crawford)

*Elachistus benefactor* Crawford, 1912:182.

*Diagnosis.* Head in front view wider than high (as in Fig. 3); gaster smooth; hind-femora cylindrical, more than  $3\times$  as long as wide; propodeal carina complete, well developed (as in Fig. 7); scutellum and axillae alutaceous; compound eye in dorsal view with hind margin reaching hind margin of occiput (Fig. 18); mandibles with 5 teeth.

This species is closely related to *thymus*. It can be separated by the eye character given above, and by the difference in the mandibles (5 teeth in *benefactor* and 6 in *thymus*).

*Hosts.* Tortricidae: *Petrove albicapitana* (Bsk.) (Northern Pitch Twig Moth), *P. comstockiana* (Fern.) (Pitch Twig Moth), *P. metallica* (Bsk.), *P. wenzeli* (Kft.). Cosmopterigidae: *Limnaecia phragmitella* Staint\*.

*Distribution.* Wash. D.C., N.Y., Minn., Utah\*, Quebec\*, Ontario\*. Burks (1979)



also cites Maryland, Ohio and British Columbia, and Peck (1963) lists Alberta or British Columbia which probably refers to the same record cited by Burks.

*Types.* This species was described from 3 syntypes, only two of which have survived. The lectotype (present designation) is point mounted with data: New York, Karner. ex. *Evetria comstockiana*. 26/VI/1901. N.Y.S. collection. USNM type no. 14809. Crawford indicated in his original description that the specimens had been reared by E. P. Felt. The head, antennae, and parts of the legs of the lectotype have been slide mounted, and labelled with the species name and the type number. The paralectotype female is also point mounted with the same data as the lectotype and has a forewing and hindwing slide mounted. Neither of these types is in good condition, having been poorly mounted originally and subsequently damaged further by Girault, who slide mounted and crushed the head of the lectotype. However, more of this specimen remains than of the paralectotype, particularly the antennae and legs.

*Other specimens examined.* 14 females, 1 male (CNC); 7 females, 1 male (USNM).

*Variation.* Size varies from 1.6 to 2.2 mm. Very little additional variation was observed in the specimens available for study. The color of the femora varied from entirely black to dark brown, and the tibiae from dark brown to yellow.

#### *Hyssopus sanninoideae* (Girault)

*Elachistus sanninoideae* Girault, 1917a:85.

*Diagnosis.* Head in front view wider than high; gaster smooth; hindfemora cylindrical, more than  $3\times$  as long as wide; propodeal carina complete, well developed, raised and flaired anteriorly (Fig. 8); scutellum and axillae alutaceous; metanotum bandlike, not expanded; petiole as long as wide.

This species is most similar to *thymus* Girault, from which it can be separated by the raised and flaired propodeal carina (propodeal carina flatter and not flaired in *thymus*), narrower metanotum (metanotum expanded medially in *thymus*), and longer petiole (petiole not longer than wide in *thymus*).

*Hosts.* Sessiidae: *Synanthedon exitiosa* (Say) (Peachtree Borer); *S. scitula* (Harr.) (Dogwood Borer); *S. pictipes* (G. & R.)\* (Lesser Peachtree Borer).

*Distribution.* Ark., Ga.\*, Virg., N.C.\* Both Burks (1979) and Peck (1963) list records from Connecticut.

*Types.* Lectotype female (present designation) on point with data: Arkansas, Fayetteville. July 23, 1916. ex. *Sanninoidea exitiosa*. USNM type no. 20758. Girault cites B. Becker as collector in his original description. 3 female paralectotypes and 1 male paralectotype with same type numbers, but no other date. All five specimens cited by Girault as types have survived and are in relatively good shape. The lectotype is intact, and I have slide mounted the one antenna and labelled it with the same data as the rest of the type.

*Other specimens examined.* 67 females, 7 males (USNM).

*Variation.* Size ranges from 1.8 to 2.0 mm. Body color is generally black, except for the following: the head occasionally is reddish brown; the scape and funicle range from yellow to light brown; the coxae from brown to black; the femora and tibiae from yellow to brown, usually with the tips lighter; the gaster is usually dark brown,

with the anterior  $\frac{1}{4}$  slightly lighter, especially in the males. The sculpture of the scutellum and scutum varies slightly, fading in some specimens to nearly smooth medially and posteriorly. The metanotum in some specimens is very narrow medially, and the foveae along the ventral edge may be quite pronounced in some specimens but quite small in others. The nucha may be smooth or slightly rugose. The degree to which the propodeal carina is raised and flaired anteriorly varies slightly but is always quite distinct.

### **Hyssopus clypealis, new species**

*Holotype female.* Length 1.5 mm. Color as follows: head, and thorax black; scape, legs yellow; flagellum, gaster brown. Head in frontal view slightly wider than high (45:38); ocelli arranged in isosceles triangle, POL  $2 \times$  OOL; eye height slightly more than  $\frac{1}{2}$  head height; width of eye in lateral view  $\frac{2}{3}$  as wide as head (16:24), surface apparently asetose; frons and vertex lightly alutaceous, becoming coriaceous below toruli; genae nearly smooth, very lightly alutaceous; clypeus produced forward and overhanging oral cavity (Fig. 14); mandibles with 2 large teeth and 4 smaller teeth; area dorsad of oral cavity with scattered silvery setae; antennae as in Figure 13; scutum coriaceous, side lobes with single enlarged seta; scutellum, and axillae coriaceous; pronotum as long as wide; scutellum longer than wide (24:18); metanotum sloping away from scutellum; propodeum with complete median carina, area laterad of carina lightly striate to alutaceous; lateral spiracular area below plain of median propodeum; callus with numerous setae; prepectus smooth; mesepisternum alutaceous; mesepisternal-mesepimeral suture acutely angled, foveolate over entire length; mesepimeron smooth, suture incomplete; petiole barely as long as wide; gaster smooth, about as long as wide; ovipositor sheaths reaching slightly past tip; hindcoxae slightly longer than wide; femora cylindrical, not swollen medially, more than  $3 \times$  as long as wide; submarginal vein with 8 setae; uncus with 4 sensillae.

*Male.* Unknown.

*Diagnosis.* Head in front view wider than high; gaster smooth; forefemora cylindrical, more than  $3 \times$  as long as wide; propodeal carina complete, well developed (as in Fig. 7); scutellum coriaceous; clypeus produced forward over oral cavity (Fig. 14).

This species is closest to *thymus* Girault and *sanninoideae* (Girault). It is most easily separated by the clypeal character given above (clypeus margin straight, not produced over oral cavity in *thymus* and *sanninoideae*). In addition, the coxae and legs in *clypealis* are concolorous yellow whereas in the other species the coxae and femora or tibiae are almost always marked with some brown or black (some smaller specimens of *thymus* reared from *Coleophora* spp. have been seen with yellow legs and coxae).

*Hosts.* Unknown.

*Distribution.* Known only from the type locality: Iowa.

*Types.* Holotype female on point (single antenna and pair of forewings mounted on slide) with data: Iowa, Muscatine Co., Oct. 4, 1952. J. C. Schaffner. 2 female paratypes with same data as holotype.

*Etymology.* The specific epithet refers to the enlarged clypeus found in the females of this species.

***Hyssopus aaba*, new species**

*Holotype female.* Length 2.5 mm. Color black except tibiae and tarsi brown. Head in frontal view wider than high (32:27); ocelli arranged in isosceles triangle; POL  $3.5 \times$  OOL; eye height  $\frac{2}{3}$  head height; width of eye in lateral view more than  $\frac{2}{3}$  head width (32:24), surface covered with erect white setae; frons, vertex, and genae alutaceous to coriaceous, except becoming smooth at scrobes; vertex with numerous erect black setae (Fig. 4); clypeal margin straight; mandibles with 2 large and 3 smaller teeth; area dorsad of oral cavity with numerous setae; antennae as in Figure 12; scutum coriaceous, side lobes with 2 enlarged erect setae near notauli (Fig. 10); scutellum coriaceous, axillae nearly smooth; pronotum slightly wider than long (50:40); scutellum longer than wide (40:27); metanotum sloping slightly; propodeum smooth with complete median carina; lateral spiracular area below plane of median area; callus with numerous silvery setae; prepectus very lightly alutaceous, becoming coriaceous ventrally; mesepisternum alutaceous; mesepisternal-mesepimeral suture angled, foveolate ventrally; mesepimeron nearly smooth, very lightly alutaceous, suture complete; petiole slightly wider than long; gaster smooth, longer than wide (65:35); ovipositor sheaths reaching slightly past tip; hindcoxae about as long as wide; submarginal vein with 14 setae, uncus with 5 sensillae (Fig. 17).

*Male.* Unknown.

*Diagnosis.* Head in frontal view wider than high; gaster smooth; hindfemora cylindrical, more than  $3 \times$  as long as wide; median propodeal carina well developed, raised from surface (as in Fig. 7); gaster smooth; vertex with numerous erect black setae (Fig. 4); eyes with numerous silver setae; side lobes of scutum with 2 enlarged setae (Fig. 10); uncus with 5 sensillae (Fig. 17).

This species is most easily confused with *benefactor* (Crawford) and *thymus* Girault. It can be separated by the following: eyes distinctly covered with silvery setae (eyes nearly bare in other species); vertex with numerous erect black setae (vertex covered by shorter usually silver setae in other species); uncus with 5 sensillae (uncus 4 sensillae in other species); and side lobes of scutum with 2 enlarged setae near the notaular margin (other species have only a single large seta on the midlobe near the notauli).

*Hosts.* Sessiidae: *Synanthedon sequoiae* (Hy. Edw.) (Sequoia Pitch Moth).

*Distribution.* Known only from the type locality: California.

*Types.* Holotype female on point (antenna and forewing mounted on slide) with data: California, Los Gatos. Aug. 4, 1970. ex. *Vespimima sequoiae* on pine. Three female paratypes with same data as holotype.

*Etymology.* The specific epithet is an arbitrary combination of letters.

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## ANTAGONISM OF ENTOMOGENOUS FUNGAL EXTRACTS TO THE DUTCH ELM DISEASE FUNGUS, *CERATOCYSTIS ULMI*

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**Abstract.**—Culture filtrates extracted from two species of entomogenous fungi, *Metarhizium anisopliae* and *Nomuraea rileyi*, and a commercial toxin, beauvericin, demonstrated antimycotic activity to two strains of the causal agent of the Dutch elm disease, *Ceratocystis ulmi*. Extracts of *Beauveria bassiana*, as tested, displayed no antagonism to *C. ulmi*. Beauvericin was antagonistic only to the aggressive strain of *C. ulmi*, while the entomogenous fungal species were antagonistic to both the aggressive and nonaggressive strains of *C. ulmi*. *M. anisopliae* produced the highest level of antagonism to *C. ulmi*, and the aggressive strain of *C. ulmi* showed greater sensitivity to antagonism than the nonaggressive strain. Extracts from both strains of *C. ulmi* produced no antagonism against the three species of entomogenous fungi.

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The possible use of entomogenous fungi to control the insect vector of Dutch elm disease (DED) was supported by reports of fungal pathogenicity to elm bark beetles (Coleoptera: Scolytidae) (Barson, 1976, 1977; Doane, 1959; Doberski, 1981). Agents used to control the insect vector may also interact secondarily with the fungal pathogen. Alternatives to chemical and classical biological control of *Scolytus multistriatus*, the insect vector of Dutch elm disease, must also take into account the possible antagonism between *Ceratocystis ulmi*, the causal agent of DED, and entomogenous fungi. Several species of nonentomogenous and entomogenous fungi have demonstrated antagonism to both the aggressive and nonaggressive strains of *Ceratocystis ulmi* (Gemma et al., 1984; Gibbs and Smith, 1978; Holmes, 1954; Webber, 1981). To determine the basis for this activity, culture filtrates of three species, *Beauveria bassiana*, *Metarhizium anisopliae*, and *Nomuraea rileyi* were prepared and their antimycotic activity tested against *C. ulmi* along with beauvericin, the commercially prepared toxin from *B. bassiana*.

### METHODS

Culture filtrates from *Beauveria bassiana* (Bals.) Vuill. ATCC18514, *Metarhizium anisopliae* (Metsch.) Sorokin ATCC22099, and *Nomuraea rileyi* (Farlow) Samson (obtained from C. Ignoffo, USDA, Columbia, Missouri) were evaluated for their capacity to inhibit the growth of two strains of the DED fungus, *Ceratocystis ulmi* (Schreiber and Addison original strain) aggressive (A) and *Ceratocystis ulmi* non-aggressive strain (NA). The cultures were incubated in 250 ml Erlenmeyer flasks containing 30 ml potato dextrose broth (PDB) (with the exception of *N. rileyi* which was grown on Sabouraud's maltose broth plus 1% yeast extract) at ambient temperature in complete darkness. For each species, 30 flasks were inoculated with an agar



Table 1. The effect of time and concentration on the inhibition of two strains of *Ceratomyces ulmi* by filtrates of cultures of entomogenous fungi.

Age of culture when filtrate was extracted	2 weeks		3 weeks		4 weeks		4 weeks	
Filtrate concentration (W/V)	3.2%		3.2%		3.2%		6.4%	
Strain of <i>C. ulmi</i>	A	NA	A	NA	A	NA	A	NA
Culture filtrate								
<i>B. bassiana</i> (ATCC18514)	+	+	+	+	+	+	-	-
<i>M. anisopliae</i> (ATCC22099)	106 <sup>b</sup>	89	110	88	106	89	181	121
<i>N. rileyi</i> (Missouri strain)	+	89	109	+	99	124	148	116

<sup>a</sup> + = slight inhibition; - = no inhibition.

<sup>b</sup> = zone of inhibition (mm<sup>2</sup>).

plug (7 mm diam) cut with a flamed cork borer from the surface of a 48 hr. mycelium on water agar. Culture filtrates were then collected at intervals of two, three, and four weeks after inoculation.

Culture filtrates were prepared by filtering the contents of 10 flasks for each fungal species through a Nalgene® Sterilization Filter Unit (pore size 0.45  $\mu$ m), and dehydrated by freeze-drying. The residue was dissolved in sterile 0.01% Triton-X solution to produce a concentration of 3.2% (W/V). Uninoculated aliquots of culture broths were treated similarly and used as controls. The residue from the filtrate collected at four weeks was reconstituted to produce two final filtrate concentrations of 3.2% and 6.4% (W/V).

For the evaluation of filtrate activity, a mycelial mat of *C. ulmi* (strain A or NA) was homogenized in 30 ml of sterile 0.01% Tween 80 solution in a sterile Waring blender. One ml aliquots of the slurry were then spread on the surface of appropriate agar medium in a 100  $\times$  15 mm Petri dish. Four wells (1  $\times$  8 mm) were cut in the agar surface of each plate with a sterile cork borer and 0.1 ml sample of a given filtrate was transferred to each of three wells; an appropriate control was placed in well 4. Five replicates were made for each filtrate tested. Zones of inhibition, if produced, were measured at the end of four days. The antimycotic activity of culture filtrates of *C. ulmi* (A and NA) was determined similarly. Beauvericin (Sigma Chemical Co. B7510) dissolved in methanol at a concentration of 0.5 mg/ml (W/V) was tested in the same manner against *C. ulmi* (A and NA).

## RESULTS

Antimycotic activity against both strains of *C. ulmi* was demonstrated by culture filtrates produced from *M. anisopliae* and *N. rileyi*, respectively (Table 1) (Fig. 1). Filtrates from older cultures did not produce greater zones of inhibition when compared with those of filtrates from younger cultures, but doubling the concentration of the four week old filtrates from *M. anisopliae* and *N. rileyi* did significantly increase the zones of inhibition (Table 1). Extracts from *M. anisopliae* cultures produced the highest level of inhibition against both strains of *C. ulmi* with the A strain more susceptible. *C. ulmi* extracts (A and NA) produced no antimycotic activity against



Fig. 1. The aggressive strain of *Ceratocystis ulmi* growing on the surface of potato dextrose agar in a Petri plate. Three of the wells (e) contain a filtrate (concentration 6.4%) of a four week culture of *Metarhizium anisopliae* and are surrounded by a zone of inhibition (i). The control well (c) contains a filtrate prepared from sterile liquid medium.

*B. bassiana*, *M. anisopliae*, and *N. rileyi*. Beauvericin produced a slight inhibition zone against *C. ulmi*-NA, but an inhibition zone of 110 mm<sup>2</sup> resulted in tests against *C. ulmi*-A.

#### DISCUSSION

Fungal extracts of two entomogenous culture filtrates showed clear antimycotic activity against *C. ulmi*; furthermore, the activity increased with the concentration. Failure of the filtrate from four week old mycelia to produce a larger zone of inhibition than the filtrate from two week old mycelia seems to indicate that antimycotic substances are not continuously produced during mycelial growth in culture. Although several studies have reported the isolation of several different metabolites from *C. ulmi*, including phenolics, phytotoxic glycopeptides, and a wilt-inducing toxin, ceratoulmin (Claydon et al., 1974; Strobel and Lanier, 1981; Takai, 1974), culture extracts of *C. ulmi* did not demonstrate any antimycotic activity to those species of entomogenous fungi tested. These results support the potential of these entomogenous

fungi as biological control agents of the pathogen of DED as well as for control of its vector, the elm bark beetle.

Differences between the aggressive and nonaggressive strains of *C. ulmi* in response to fungal extracts and beauvericin may result from each strain's genetic differences which alter their response to external factors (Pusey and Wilson, 1979). Additionally, the effect of such factors as strain variation, temperature, degree of aeration, nature of the medium, and moisture content of the medium (Ciegler, 1977) on the production of antimycotic substances by entomogenous fungi needs to be examined carefully.

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MELANISM IN *PHIGALIA TITEA* (CRAMER)  
(LEPIDOPTERA: GEOMETRIDAE) IN SOUTHERN  
NEW ENGLAND: A RESPONSE TO  
FOREST DISTURBANCE?

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*Abstract.*—The typical and melanic morphs of *Phigalia titea* (Cramer) exhibited different background preferences in an experimental apparatus, the typicals behaving like species known to rest on many tree species in nature, and the melanics behaving like species known to rest preferentially on white birches. Field observations of *Cosymbia pendulinaria* Guenée indicate that some melanic moths are cryptic on gray (*Betula populifolia*) and paper (*B. papyrifera*) birches. It is suggested that the successional characteristics of these birches in New England forests may provide the basis for a recurring advantage of melanism, and that increases in the abundance of these birches since colonial settlement may explain the melanism seen in the region today.

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Industrial melanism in moths has become a standard textbook example of evolution in action. The traditional explanation of this phenomenon was developed by Kettlewell and his associates working in England with the peppered moth, *Biston betularia* (L.). This explanation involves a series of observations including well-documented changes in the frequencies of the melanic morphs of this species, a simple genetic basis for the melanic condition, an environmental change (darkening of tree trunks) to which the moths are apparently responding, and a selective agent (birds preying on resting moths) which presumably directs the evolutionary process (Kettlewell, 1955a, 1956, 1973). Recently, however, increasing skepticism as to the general adequacy of this explanation has emerged (Bishop, 1972; Creed et al., 1973; Sargent, 1974; Bishop and Cook, 1975; Lees and Creed, 1975; Steward, 1977a, b; Lees, 1981; Hailman, 1982), based in part on reports of rural melanism in North America (Klots, 1964, 1966, 1968a, b; Sargent, 1971, 1974, 1983; Jones, 1977; West, 1977; Manley, 1981). A particular problem is posed by experimental results which indicate that melanic individuals of several species prefer light over dark backgrounds (Sargent, 1968, 1969; Lees, 1975; Steward, 1976, 1977c), unlike the dark over light background preference reported in similar experiments with melanic *B. betularia* (Kettlewell, 1955b; Boardman et al., 1974; Kettlewell and Conn, 1977).

The present paper reports results of further background preference tests with *Phigalia titea* (Cramer) (Lepidoptera: Geometridae), a species whose melanic morph has previously been shown to prefer white over black backgrounds (Sargent, 1969). These new results indicate that melanic *P. titea*, unlike their typical counterparts, behave like species that are known to rest on white birches (*Betula papyrifera* Marshall and *B. populifolia* Marshall) in nature. These experimental findings, together with field observations of the birch-resting geometrid, *Cosymbia pendulinaria* Guenée, suggest

that melanic moths may be cryptic on very light trees like birch and aspen because of the numerous black patches which also characterize these trees.

White birches and aspens are early, successional species in New England forests and I suggest that natural disturbances that favor these trees may have provided recurring opportunities for the rise and spread of melanism in moths in the past. It follows that the extensive human disturbance of the forest since colonial settlement could be a factor in the incidence of melanism we see today.

#### METHODS AND MATERIALS

The experimental apparatus used in this study is similar to one used previously in black vs. white background preference tests (Sargent, 1968, 1969a, b, 1973; Lees, 1975), but here consisted of four backgrounds: white, black, horizontally striped, and vertically striped. Each of the four backgrounds was made from a piece of white blotting paper, unmarked to provide the white background, and marked with a black marking pen to provide the striped and black backgrounds. The striped backgrounds consisted of repeating sequences of 0.5 mm, 2.0 mm, and 10.0 mm black lines, the lines separated from one another by 7.0 mm white spaces (the backgrounds overall being 65% white and 35% black). The four pieces of blotting paper were formed into a cylinder of alternating solid and striped backgrounds, and this cylinder was set into a plywood box (35.6 cm square by 48.3 cm high) which was covered with a pane of clear window glass. The entire apparatus was set out in a wooded area near my home in Leverett, Massachusetts.

The moths to be tested were captured during the seasons of 1981–1983 at 150-watt incandescent spotlights (Westinghouse outdoor projector) or a 15-watt fluorescent blacklight tube (General Electric F15T8 BL). The moths were placed into the experimental apparatus after their capture at night, and their background selections were recorded shortly after daybreak on the following morning.

The statistical test used in all comparisons of background selections in this apparatus was the  $R \times C$  test of independence using the G-test (Sokol and Rohlf, 1969).

*Phigalis titea* is an early spring species, with males on the wing in Leverett during March and April (females have rudimentary wings and do not fly). Typical *P. titea* are light gray with strongly contrasting black lines, while melanics are evenly blackish overall (both morphs are illustrated in Remington (1958) and Sargent (1983). The melanic morph, "deplorans," was named in 1938 (Franclemont), though an early specimen was described in 1869 (Minot). Owen (1961, 1962) has discussed the history of melanism in this species, noting that early records of the melanics were not concentrated near industrial centers. Lees (1971) has made a similar point regarding melanism in the closely related *P. pilosaria* Schiff. in England. In Leverett, melanics have comprised 18.8% of the 4,078 male *P. titea* captured over the past 16 years (Sargent, 1983).

#### RESULTS AND DISCUSSION

The typical and melanic morphs of *P. titea* exhibited significantly different background preferences in the present experimental apparatus, the typicals preferring the horizontally and vertically striped backgrounds, and the melanics preferring the horizontally striped and white backgrounds ( $P < 0.05$ ) (Fig. 1).



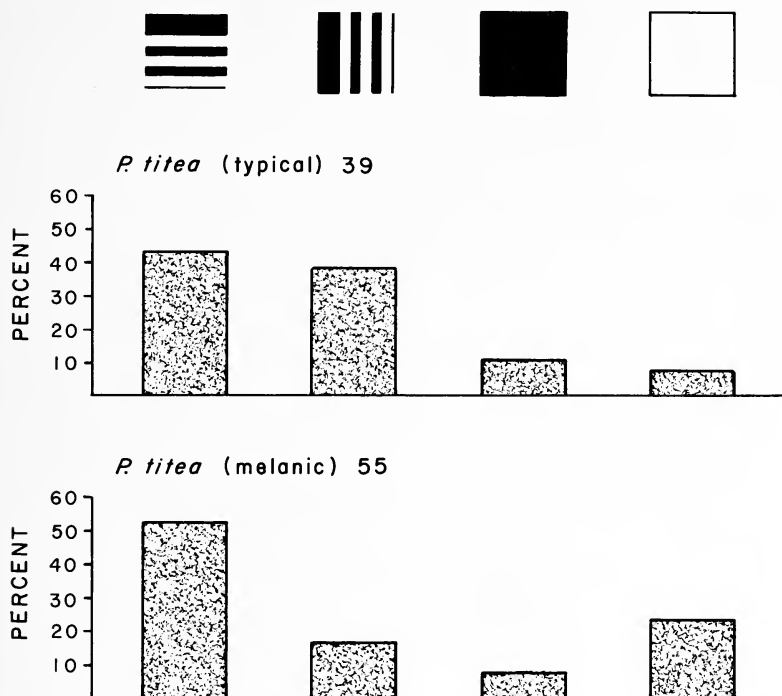


Fig. 1. The distribution of typical and melanic *Phigalia titea* in an experimental apparatus providing a choice among horizontally striped, vertically striped, black, and white backgrounds. The numbers of individuals tested are given after the morph designations.

The behavior of the typical *P. titea* was similar to that of a number of light, bark-like geometrids that are known to rest by day on the trunks of a wide variety of tree species in the Leverett area (Sargent and Keiper, 1969; Sargent, unpubl.). The background choices of one such species, *Anacamptodes ephyraria* (Walker), are depicted in Figure 2, and these did not differ from those of the typical *P. titea* ( $P > 0.90$ ). The behavior of the melanic *P. titea*, on the other hand, resembled that of several very pale geometrids that prefer to rest by day on white birches (Sargent and Keiper, 1969; Sargent, unpubl.). *Cladara atroliturata* (Walker) is one such species, and its background selections in the experimental apparatus (Fig. 2) did not differ from those of the melanic *P. titea* ( $P > 0.30$ ).

These experimental results suggest that the two morphs of *P. titea* might differ with respect to their resting habits in nature. Unfortunately, as with many species exhibiting melanism (Mikkola, 1979), there are no published observations of *P. titea* in natural resting situations. I have been unable to find individuals of either morph at rest in the Leverett area, though my searches to date have concentrated on oaks, as I have received one report of typical *P. titea* resting on *Quercus alba* L. in southwestern Massachusetts (R. D. Childs, pers. comm.). The possibility of a birch-resting preference for the melanics had not occurred to me prior to the present analysis, though this possibility should guide future search efforts.

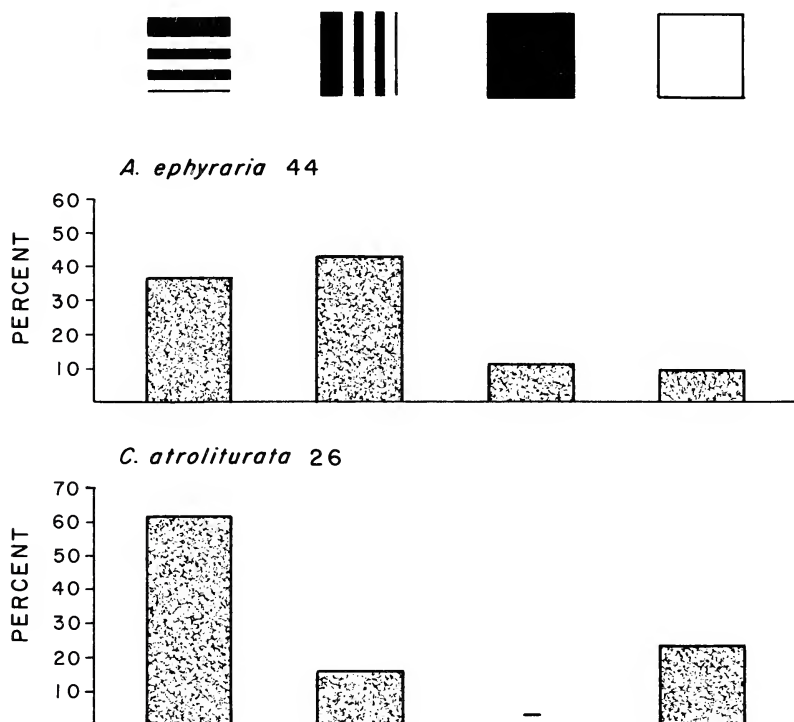


Fig. 2. The distribution of *Anacamptodes ephyraria* and *Cladara atroliturata* in an experimental apparatus providing a choice among horizontally striped, vertically striped, black, and white backgrounds. The numbers of individuals tested are given after the species names.

I have found many specimens of another local geometrid, *Cosymbia pendulinaria* Guenée, resting on white birches (Sargent and Keiper, 1969; Sargent, unpubl.), and further consideration of this species may be informative. *Cosymbia pendulinaria* is double-brooded in Leverett, but has a later flight season (May–August) than *P. titea*. The moth is typically white with variable amounts of blackish dusting, but occurs as well in a melanic morph, “nigricaria” (Rothke, 1920), which is very dark gray or blackish. This melanic morph comprises about 5% of the species population in Leverett.

Both morphs of *C. pendulinaria* prefer white over black backgrounds in experimental tests (Sargent, 1968); and in the present apparatus, both exhibited similar preferences ( $P > 0.80$ ) for the horizontally striped and white backgrounds (Fig. 3). Their behavior in this apparatus was similar then to that of the birch-resting *C. atroliturata* ( $P$ 's  $> 0.10$  and  $> 0.30$  for the typical and melanic morphs respectively) and to the melanic *P. titea* ( $P$ 's  $> 0.30$  and  $> 0.50$  for the typical and melanic morphs, respectively), but differed significantly from the typical *P. titea* ( $P$ 's  $< 0.01$  for both morphs).

My field observations indicate that both morphs of *C. pendulinaria* rest prefer-

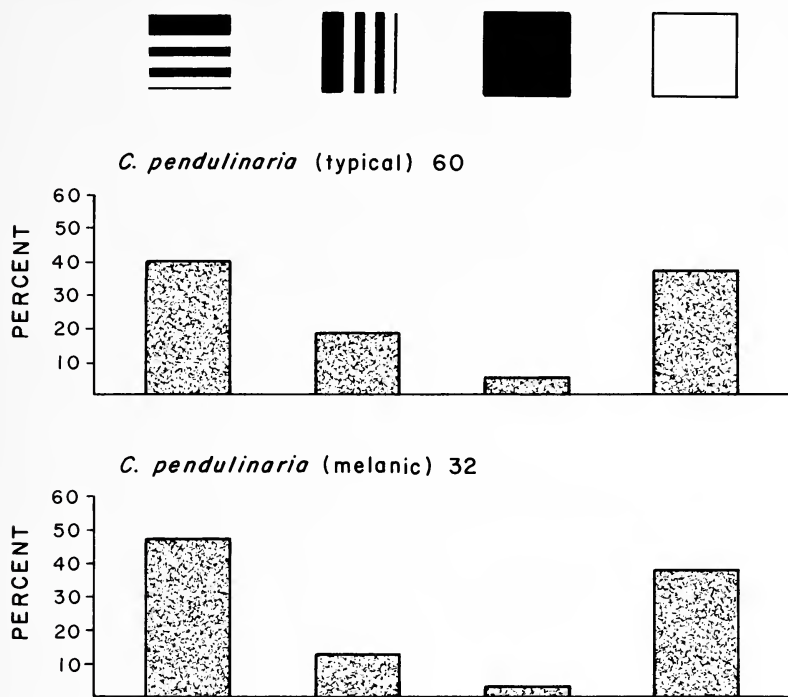


Fig. 3. The distribution of typical and melanic *Cosymbia pendulinaria* in an experimental apparatus providing a choice among horizontally striped, vertically striped, black, and white backgrounds. The numbers of individuals tested are given after the morph designations.

entially on white branches (ca. 98% of over 200 observations of typicals, and all 13 observations of melanics). Both morphs appear cryptic on these trees, though for different reasons. Typicals tend to match the predominantly white backgrounds that these birches provide; and melanics, though conspicuous with respect to their immediate surroundings, tend to resemble the black patches that characterize these trees, when viewed from a more distant perspective. Some melanic *C. pendulinaria* (5/13) were found abutting black patches on birches, and this positioning seemed to enhance the moths' crypsis by disrupting their outlines and making them appear as irregular extensions of the black patches with which they were associated. There is some evidence for a similar tendency in *Phigalia pilosaria*, in that both morphs of this species show a highly significant tendency to rest with their heads exactly at the black boundary when tested in a black vs. white background choice apparatus (Lees, 1975).

The results of the present study suggest that some melanic moths may be adapted to exploit white backgrounds that are variegated with black, rather than the uniformly dark or black backgrounds that are suggested by the traditional explanation of industrial melanism. In New England, the trees that most clearly provide such white and black variegated backgrounds are the two common white birches, paper birch

(*Betula papyrifera*) and gray birch (*B. populifolia*). Both of these trees have chalky white bark with prominent, triangular black patches (these patches being especially common on *B. populifolia*) (Harlow et al., 1978). (The aspens, *Populus tremuloides* Michx. and *P. grandidentata* Michx. have similar, though less strikingly variegated bark surfaces, and a case for their role in the maintenance of melanic polymorphisms in moths might also be developed.)

*Betula papyrifera* and *B. populifolia* are relatively short-lived, shade intolerant species which exhibit the "exploitative strategy" in forest succession, persisting for only a single generation (ca. 35 years in the case of *populifolia*, and ca. 75 years in the case of *papyrifera*) in undisturbed situations (Harlow et al., 1978; Bormann and Likens, 1979). Pollen and seed data indicate that both species have been present in New England for at least 10,000–12,000 years, and that natural disturbances (e.g., hurricanes, fires) have intermittently provided locally favorable conditions for their occurrence (Patterson, unpubl.). However, neither species seems to have been common in the so-called climax forests that characterized much of New England prior to the arrival of Europeans in the 17th and 18th centuries (Bromley, 1935; Siccama, 1971; Lorimer, 1977).

Since colonial settlement there has been a substantial increase in the frequencies of these birches in response to man's disturbance of the forests (clearing, logging) and his subsequent abandonment of agricultural lands (Harlow et al., 1978; Bormann and Likens, 1979). Palynological documentation of this increase is clearest for gray birch (*B. populifolia*), since this species can be separated from other *Betula* on the basis of its small pollen size (Leopold, 1956; Patterson, unpubl.). A trend of increasing abundance of gray birch since local settlement characterizes pollen records throughout central and southern New England, and it seems safe to conclude that gray birch is more abundant there today than at any other time in the past 1,000 years (Patterson, unpubl.).

If melanism in some moth species is a response to the availability of suitable resting sites provided by white birches, then the recent increase in the abundance of these trees may provide an explanation for the corresponding increase in the incidence of melanism. Furthermore, the transitory characteristics of these early successional tree species would provide the basis for a recurring adaptive advantage of the melanic condition. It is widely recognized that some sort of recurring advantage is implied by the fact that melanism in moths is almost always a dominant trait (Kettlewell, 1973; Ford, 1975; Hailman, 1982).

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## NEWLY RECOGNIZED SYNONYMS, HOMONYMS, AND COMBINATIONS IN THE NORTH AMERICAN MIRIDAE (HETEROPTERA)

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*Abstract.*—In the North American Miridae, nine new synonyms for species and one for a genus are proposed, replacement names are given for two homonyms, ten species are transferred to different genera, and six lectotypes are selected.

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Recent study of the literature and type material in several museums has revealed a number of synonyms, homonyms, and incorrectly placed species. These discoveries are here presented to make them available for entry in the forthcoming catalog of the Heteroptera of the continental United States and Canada. In this paper, I propose nine new synonyms for species and one for a genus, offer replacement names for two homonyms, transfer ten species to different genera, and select six lectotypes.

The following abbreviations are used for institutions cited in this paper: BM (British Museum [Natural History]), London; CAS (California Academy of Sciences, San Francisco); CU (Cornell University, Ithaca, New York); NRS (Naturhistoriska Riksmuseet, Stockholm); PDA (Pennsylvania Department of Agriculture, Harrisburg); PU (Purdue University, West Lafayette, Indiana); USNM (United States National Museum of Natural History, Washington, D.C.); UZMH (Universitetets Zoologiska Museem, Helsinki); ZIL (Zoological Institute, Leningrad).

### *Criocoris saliens* (Reuter)

*Strongylotes saliens* Reuter, 1876:88.

*Criocoris canadensis* Van Duzee, 1912:511 (synonymized by Blatchley, 1926:961).

*Criocoris saliens* Van Duzee, 1914:29.

*Atractotomus flavotarsus* Johnston, 1939:129; Froeschner, 1963:4. **New Synonymy.**

*Criocoris saliens* is a widespread phyline ranging from Ontario and Massachusetts, south to Georgia, and west to Saskatchewan, California, and Texas (Carvalho, 1958; Henry and Smith, 1979; Kelton, 1980). The known hosts of *saliens* are *Galium aparine* L. (Knight, 1941), *G. boreale* L. (Kelton, 1980), and *G. mollugo* L. (Wheeler et al., 1983).

*Atractotomus flavotarsus* was described from a long series of specimens taken "breeding" on *Houstonia angustifolia* Michx. at Huntsville, Texas (Johnston, 1939). Froeschner (1963) included this species in his key to the genus *Atractotomus* based on characters from the original description. There is no other record for this species in the literature.

I have compared paratypes of *flavotarsus* (USNM) to material of *saliens* from the

eastern United States and find them indistinguishable. Both *Houstonia* and *Galium* belong to the family Rubiaceae.

*Dagbertus fasciatus* (Reuter)

*Lygus fasciatus* Reuter, 1876:72.

*Dagbertus fasciatus*: Kelton, 1955:284; Leston, 1979:377; Carvalho and Fontes, 1983: 158.

*Dagbertus fasciatus* was described from South Carolina (Reuter, 1876). There has been considerable confusion over the identity of this species and the closely related *Dagbertus olivaceus* (Reuter, 1907) described from Jamaica. Knight (1917) and Blatchley (1926) suggested that *olivaceus* was a junior synonym of *fasciatus*. Kelton (1955), however, studied male parameres and concluded that both were distinct species of the genus *Dagbertus*, and later (1974) suggested that *Lygus hospitus* Distant, described from Mexico, was the senior synonym of *olivaceus* Reuter. Leston (1979) agreed that two species were involved, but disagreed with Kelton claiming that he reversed the figures of male genitalia of *fasciatus* and *olivaceus*, and placed *hospitus* as a junior synonym of *fasciatus*, not as a senior synonym of *olivaceus*.

Apparently no one has compared type material of *fasciatus* and *olivaceus* to fully clarify the above confusion. I have examined syntypes and hundreds of specimens of both species from the eastern United States and agree that Leston (1979) was correct in his interpretation of these species.

I have found that the pale second antennal segment of *fasciatus* vs. the apically black second antennal segment for *olivaceus*, first noted by Leston (1979), will consistently distinguish the two species. Additionally, on *fasciatus*, the apex of the scutellum is never reddish or infuscated, even in the darkest specimens (on extremely pale specimens there may not be any scutellar marks, but in this case, the inner margin of the clavus nearly always is infuscated or clouded with brown); whereas on *olivaceus*, the entire scutellum, or most often, the apical  $\frac{1}{3}$  is reddish, speckled with red, or fuscous (on extremely pale specimens there may not be any markings but, in this case, the clavus never is infuscated or clouded with brown).

I also have examined the holotype female (BM) of *hospitus* collected from Chilpancingo, Guerrero, Mexico. Unfortunately, the specimen is a light-colored female, making comparison of male genitalia impossible. The BM specimen has entirely pale 2nd antennal segments, and the scutellum is pale with fuscous or brownish clouds along the inner margin of the clavus, indicating that it is conspecific with or very close to *fasciatus*. Carvalho and Fontes (1983) overlooked Kelton (1974) and Leston's (1979) synonymical treatment of *hospitus*. They illustrated male genitalia of what they considered is *hospitus* and recognized it as a valid species. In this paper, Carvalho and Fontes' (1983) interpretation is followed until their material can be restudied and compared to that of *fasciatus* to clarify the discrepancy.

To insure nomenclatural stability for the species *fasciatus* and *olivaceus*, I am designating the following lectotypes.

*Dagbertus fasciatus*.—Lectotype female: Label 1, "Carolin. mer."; 2, "Belfrage"; 3, "Typus" (red); 4, "*Lygus fasciatus* Reut. Typ." (folded); 5, "274 83" (pink); 6, "Riksmuseum Stockholm" (blue); 7, "Lectotype: ♀. *Lygus fasciatus* Reuter, by T. J. Henry" (red) [NRS]. Paralectotype: No other syntypes found.

*Dagbertus olivaceus*.—Lectotype male: Label 1, "Mandev'le, Ja., Apr. 06"; 2, "Van Duzee Collector"; 3, "8"; 4, "*Lygus olivaceus* n. sp., O. M. Reuter det."; 5, "Mus. Zool. H:fors, Spec. typ. No. 9924, *Lygus olivaceus* Reut."; 6, "Lectotype: ♂, *Lygus olivaceus* Reuter, by T. J. Henry" (UZMH). Paralectotypes: 4 males (1 CAS, 3 UZMH), 4 females (3 CAS, 1 UZMH), 1 [sex?], same data as for lectotype.

*Dagbertus semipictus* (Blatchley), **New Combination**

*Bolteria semipicta* Blatchley, 1926:743; Knight, 1928a:131; Knight, 1971:94.

*Dagbertus parafasciatus* Maldonado, 1969:36; Leston, 1979:377 (as synonym of *fasciatus* [Reuter]); Carvalho and Fontes, 1983:170. **New Synonymy.**

Blatchley (1926) described *Bolteria semipicta* from a single male taken at porch light at Dunedin, Florida. Knight (1928a), in reviewing the genus *Bolteria*, commented that "The relatively narrow vertex which in width does not equal the length of the first antennal segment, strongly suggests that this species may not belong in the genus *Bolteria*." In a later revision of *Bolteria*, Knight (1971) re-stated his doubts about the generic placement of *semipicta* and provided a key to help separate the 14 species known in the genus.

Maldonado (1969) described *parafasciatus* from a large series of specimens collected in Puerto Rico. Leston (1979), without comment, considered *parafasciatus* a junior synonym of *fasciatus* (Reuter). Carvalho and Fontes (1983), apparently in overlooking Leston's synonymical treatment, considered *parafasciatus* a distinct species.

I have examined Blatchley's holotype of *semipicta* and find it clearly a member of the genus *Dagbertus* Distant. Additionally, I have studied the lectotype of *fasciatus* (see type designation of *fasciatus* in this paper) and the holotype (USNM) and several paratypes (USNM) of *parafasciatus*, and agree with Carvalho and Fontes (1983) that these two species are distinct. *Dagbertus parafasciatus*, however, is conspecific with *semipictus* and, thus, a junior synonym.

*Dagbertus semipictus* can be separated from *fasciatus* in the U. S. fauna in having the 2nd antennal segment slightly longer than the basal width of the pronotum (in *fasciatus* the 2nd antennal segment is shorter than the basal width of the pronotum), the apex of the tylus fuscous (tylus pale on *fasciatus*), the sides of the thorax and abdomen with a wide, fuscous stripe (*fasciatus* has, at most, red flecks), and the base of the pronotum with a wide, transverse, brown to fuscous band.

With the above synonymy, *semipictus* is now known to occur in Florida and Puerto Rico. I have collected large numbers of this species in Dade and Monroe counties, Florida on the flowers of *Hippocratea volubilis* L. (Hippocrateaceae) and at black light traps. Maldonado (1969) listed the majority of his specimens from the flowers of *Tecoma stans* (L.) Juss. (Bignoniaceae).

*Dagbertus irroratus* (Blatchley), **New Combination**

*Lygus* (*Neolygus*) *irroratus* Blatchley, 1926:775.

*Lygus irroratus*: Carvalho, 1959:122.

*Lygocoris irroratus*: Kelton, 1974:379.

Blatchley (1926) described *irroratus* from a single female collected at Royal Palm

Park, Florida. He placed it in the subgenus *Neolygus* because of the finely punctate pronotum. Kelton (1974), in preparation for his revision of the North American lygus bugs (Kelton, 1975), tentatively transferred *irroratus* from *Lygus* to *Lygocoris* based on the original description. He noted that he had not been able to locate the type and that it was possible that the species might even belong in the subfamily Orthotylinae or Phylinae.

I have been able to study the holotype of *irroratus* (PU) and find that it does not belong in either *Lygus* Hahn or *Lygocoris* Knight, and that it is clearly a member of the subfamily Mirinae. Unfortunately, the specimen is a female, so male genitalia cannot be studied, but based on the general body form, impunctate dorsum, head structure, peculiar emargination of the eyes, and position of the antennae, *irroratus* is nearest to species of *Dagbertus* Distant and *Taylorilygus* Leston. Slater and Baranowski (1978) separated *Dagbertus* from *Taylorilygus* by the relative length of the 3rd antennal segment to the length of the head. On the basis of this character, *irroratus*, with a very short 3rd antennal segment, should be placed in *Dagbertus*.

The overall pale brown coloration flecked with numerous scattered paler spots (spots less evident on clavus and corium) on the dorsum and ventral surface, the pale brown antennal segments with segment III very short, and the somewhat reddish tibiae with large white spots will distinguish *irroratus* from all other species now included in *Dagbertus* (see Carvalho and Fontes, 1983).

#### *Europiella stitti* Knight

*Europiella stitti* Knight, 1968:46.

*Europiella franseriae* Knight, 1969:84. **New Synonymy.**

*Europiella stitti* was described from Gila Bend, Arizona based on specimens collected by L. L. Stitt in Feb. 1941 (Knight, 1968). *Europiella franseriae* also was described from Gila Bend, Arizona (Knight, 1969) based on specimens collected by L. L. Stitt in Mar. 1941 on *Franseria deltoidea* Torr. (Asteraceae). In describing *franseriae*, Knight noted that it would key out with *E. humeralis* Van Duzee, but did not mention its similarity to *stitti* or that *humeralis* keyed to two different places.

I have compared the holotypes and paratypes (USNM) of *stitti* and *franseriae* and find them clearly conspecific. It is possible that Knight forgot his earlier description of *stitti* or that his key, based in several places on the position of the rostrum (extending to posterior coxae vs. posterior trochanters), will fail to work if the specimens have the head dried in a slightly different position.

#### *Lindbergocapsus* Wagner

*Lindbergocapsus* Wagner, 1960:112. Type-species: *Lindbergocapsus lenaensis* Wagner, 1960 (original designation) [a junior objective synonym of *Orthotylus lenensis* Lindberg, 1928 (synonymized by Wagner, 1962)].

*Labopidicola* Kelton, 1979:757; Henry, 1982:1. Type-species: *Labopidea idahoensis* Knight, 1968 (original designation). **New Synonymy.**

The North American genus *Labopidicola* was described to accommodate a group of onion-feeding species that were previously placed in the genus *Labopidea* Uhler



(Kelton, 1979). Kelton (1979) gave characters to separate this group from *Labopidea*, and I (Henry, 1982) redescribed the known species, described *cepula* as new from Texas, and provided an identification key to separate the six North American species.

Recently, Dr. I. M. Kerzhner suggested to me (in lit.) that the nearctic genus *Labopidicola* was congeneric with the Asian genus *Lindbergocapsus*. After an exchange of specimens and comparison of the type-species of each genus, I agreed that *Labopidicola* is a junior synonym of *Lindbergocapsus*. Although Kelton (1979) and I (Henry, 1982) considered *Labopidicola* deserving of generic rank, at least, Kerzhner (1964 [1967]) placed *Lindbergocapsus* as a subgenus of *Orthotylus*, and Vinokurov (1979) treated *Lindbergocapsus* as a junior synonym of *Labopidea* and reduced that genus to a subgenus, also in *Orthotylus*. At present, however, I believe *Lindbergocapsus* should be maintained as a genus until a more comprehensive review of the tribe Orthotylini can be made.

*Lindbergocapsus* runs to *Labopidea* in Knight's (1941, 1968) generic keys, but can be distinguished from U. S. species of *Labopidea* by the more distinct basal carina on the vertex, the tylus or clypeus clearly visible from the dorsal aspect, the shorter, stouter rostrum, and the lack of fuscous markings on the head, calli, and antennae (Henry, 1982). Kelton (1980) provided a key to separate *Lindbergocapsus* [as *Labopidicola* from other genera occurring in the Canadian Prairie Provinces.

As a result of the above generic synonymy, the following six species are transferred to the genus *Lindbergocapsus*: *ainsliei* (Knight), 1928; *alii* (Knight), 1923a; *cepulus* (Henry), 1982; *geminatus* (Johnston), 1930; *idahoensis* (Knight), 1968; *planifrons* (Knight), 1928.

#### *Lopidea confraterna* (Gibson)

*Hadronema confraterna* Gibson, 1918:83.

*Lopidea lepidii* Knight, 1918:175. **New Synonymy.**

*Lopidea occidentalis* Van Duzee, 1918:296 (synonymized by Carvalho, 1958:86).

*Lopidea confraterna*: Carvalho, 1958:84.

*Lopidea confraterna* was described in the genus *Hadronema* Uhler from a single male taken on *Bigelovia* sp. (Rubiaceae) at Las Cruces, New Mexico. Carvalho's (1958) transfer of this orthotyline to *Lopidea* Uhler is the only other treatment.

*Lopidea lepidii* was described from numerous specimens collected on *Lepidium thurberi* Wooten (Brassicaceae) in Arizona and Colorado. Knight (1918) figured the male parameres of this species.

*Lopidea occidentalis* was described from 39 specimens collected on *Croton californicus* Muell. (Euphorbiaceae) at Palm Springs, California. Carvalho (1958) placed it as a synonym of *lepidii*.

I have examined paratypes of *lepidii* (USNM) and a single male paratype of *occidentalis* (USNM) and agree with Carvalho that *occidentalis* is a junior synonym of *lepidii*. In addition, I have studied the holotype of *confraterna* (USNM) and find that it is also conspecific with *lepidii*. All three species were described in 1918 by different authors, but Gibson's publication appeared before the others. Smithsonian Library copies received as follows: Gibson, Mar. 26, 1918; Knight, May 3, 1918. Van Duzee's paper appeared in the Oct. issue of the *Proceedings of the California Academy of Sciences*.

*Lopidea hesperus* (Kirkaldy)

*Capsus coccineus* Walker, 1873:93 (preoccupied by *Capsus coccineus* Meyer, 1843).

*Lomatopleura hesperus* Kirkaldy, 1902:252 (new name for *coccineus* Walker).

*Lomatopleura coccineus*: Distant, 1904:109.

*Lopidea reuteri* Knight, 1918:459. **New Synonymy.**

*Lopidea hesperia*: Blatchley, 1926:837.

*Lopidea hesperus*: Carvalho, 1958:85.

Walker (1873) described *Capsus coccineus* apparently from a male collected at St. John's Bluff, Florida. Kirkaldy (1902) recognized that Walker's name was preoccupied by *coccineus* Meyer and renamed the species *hesperus*. Blatchley (1926) included *hesperus* in his treatment of *Lopidea* but gave only the original description. He noted that because the original description lacked definitive diagnostic statements he could not include the species in his key.

Knight (1918) described *reuteri* from Missouri (holotype), Connecticut, Massachusetts, New Jersey, New York, Pennsylvania, and Virginia; figured male genitalia; and gave *Hamamelis virginiana* L. (Hamamelidaceae) as the host. He redescribed and keyed this species in his Miridae of Connecticut (1923b) and the Miridae of Illinois (1941). Blatchley (1926) also redescribed and keyed this species. *Lopidea reuteri* also is known from Illinois, Michigan, Mississippi, and West Virginia (Knight, 1941) and Georgia (Henry and Smith, 1979).

Knight (1965), after receiving a sketch of the male parameres and tergal process of the type of *coccineus* from W. E. China (BM), revised his earlier interpretation (Knight, 1962), and concluded that the species was very similar to *reuteri*. He noted that the slight differences shown in his drawings of the tergal process were sufficient to distinguish *hesperus* from *reuteri*. Independently, I have examined the type of *coccineus* Walker (BM) and believe that it should be considered the senior synonym of *reuteri*. I have studied the shape of the tergal process of *reuteri* on specimens from Georgia, Pennsylvania, and Wisconsin and consider the slight differences in the tergal process as noted by Knight (1965), to represent infraspecific variation. The thickness of this bladelike structure also appears slender to slightly more broadened, depending on the position in which the specimen is viewed.

Although Walker apparently had only a single specimen when describing *coccineus*, he did not specify a number. To eliminate any doubt, the following male in the BM is designated the lectotype of *coccineus* Walker: Label 1, "Type" (circular white label with green margin); 2 (folded), "152. *Capsus coccineus*"; 3, "E. Doubleday, St. John's Bluff, E. Florida"; 4, "Lectotype: *Capsus coccineus* Walker, by T. J. Henry."

*Lopidea knighti* Henry, **New Name**

*Lopidea occidentalis* Knight and Schaffner, 1975:418 (preoccupied by *Lopidea occidentalis* Van Duzee, 1918:296, a junior synonym of *Lopidea confraterna* (Gibson)—see new synonymy in this paper).

*Lopidea occidentalis* was described from 11 specimens collected in Baja California, Mexico. Because the name *L. occidentalis* is preoccupied, I am proposing the re-

placement name *knighti*, in honor of the late H. H. Knight for his extensive work on the genus *Lopidea*.

*Lopidea media* (Say)

*Capsus medius* Say, 1832:22 (LeConte ed., 1859:341).

*Lopidea media*: Uhler, 1872:412.

*Capsus floridanus* Walker, 1873:97 (synonymized by Knight, 1962:37).

*Lopidea floridana*: Distant, 1904:108.

I mention this species only because Knight (1962) did not have the type of *Capsus floridanus* Walker for study, only a few descriptive notes and a watercolor illustration of the female type of *floridanus* provided by W. E. China (BM). Recently, I re-examined the type of *floridanus* (BM) and found that Knight's synonymy is entirely correct.

*Paramixia polita* (Uhler), **New Combination**

*Psallus politus* Uhler, 1894:195.

*Sthenarus plebejus* Reuter, 1907:26; Van Duzee, 1907:28; Knight, 1926:256; Blatchley, 1926:922. **New Synonymy.**

*Orthotylellus carmelitana*: Maldonado, 1969:65 (misidentification).

*Paramixia carmelitana*: Henry and Wheeler, 1982:236 (misidentification).

Uhler (1894) described *Psallus politus* from 19 specimens collected at Chantilly, Mirabeau, and Mount Gay Estates on Grenada.

*Sthenarus plebejus* was described from several specimens taken at Mandeville, Jamaica and a single specimen taken at Tambilo, Jamaica. Later, Van Duzee (1907) reported *plebejus* from Balaclava, Jamaica, and Knight (1926) recorded it from Florida. Blatchley (1926) also recorded *plebejus* from Florida and added Cuba (based on specimens identified by Knight).

Recently, Henry and Wheeler (1982) reported Carvalho's (1948) *Paramixia carmelitana* new in the United States based on Florida specimens. They also noted that Maldonado (1969) recorded the same species from Puerto Rico.

Since the 1982 report (Henry and Wheeler), I have had the opportunity to study specimens at the BM and CAS and have discovered that *Psallus politus* and *Sthenarus plebejus* are conspecific and belong in the genus *Paramixia*. In addition, I have re-evaluated the specimens I originally identified from Florida (USNM) and specimens Maldonado identified from Puerto Rico (USNM) as *carmelitana*. By comparing syntypes of *politus* (BM, USNM) and *plebejus* (CAS) with paratypes of *carmelitana* (USNM), I find that it is *politus* that should be recognized from Puerto Rico and the United States, not *carmelitana*.

Preliminary examination indicates that *Paramixia polita* can be separated from *carmelitana* by the smaller size (males and females range from 2.04–2.20 mm) and the proportionately shorter 2nd antennal segment that is equal to or shorter than the width of the head across the eyes. USNM specimens of *carmelitana* measure 2.48–2.80 mm long, and the 2nd antennal segment is longer than the dorsal width of the

head. Also the aedeagus appears shorter and slightly more stout in *politus* than in *carmelitana*.

Although only two species of the pilophorine genus *Paramixia* are recognized from the Western Hemisphere, the large number of undetermined specimens in the USNM collection from other islands of the Caribbean and Central and South America indicates that the genus is much larger and in need of revision.

*Psallus politus*.—Lectotype male, present designation, Label 1, “102”; 2, “Mount Gay Est. (Leeward side), Grenada, W. I., H. H. Smith”; 3, “Lectotype: ♂, *Psallus politus* Uhler, by T. J. Henry” (USNM type No. 100941) [Note: the lectotype is selected from USNM material because of the poor condition of the BM specimens]. Paralectotypes: 1 male, same data as for lectotype (USNM); 1 male, Chantilly Est. (Leeward side), Grenada, W. I., H. H. Smith (USNM); 2 males (1 BM, 1 USNM), 4 females (3 BM, 1 USNM), Mirabeau Est. (Windward side), Grenada, W. I., H. H. Smith.

*Sthenarus plebejus*.—Lectotype male, present designation, (top specimen of two on a single pin): Label 1, “Mandev’le, Ja., Apr. 06”; 2, “Van Duzee Collector”; 3, “Paratype”; 4, “EP Van Duzee Collection”; 5, “Lectotype: ♂, *Sthenarus plebejus* Reuter, by T. J. Henry” (CAS). Paralectotype: 1 female on same pin (CAS).

#### *Phytocoris pleuroimos* Henry, **New Name**

*Phytocoris intermedius* Henry, 1979:6; Henry and Stonedahl, 1983:450 (preoccupied by *Phytocoris intermedius* Reuter, 1877).

I described *Phytocoris intermedius* from material collected in Georgia and North Carolina (Henry, 1979). Dr. I. M. Kerzhner (ZIL), has informed me that this name is a primary junior homonym of the palearctic *Phytocoris intermedius* Reuter, 1877, which is a junior synonym of *Phytocoris populi* (Linnaeus), 1758.

I propose the replacement name *pleuroimos*, taken from the Greek roots “pleura” meaning side and “oimos” meaning stripe. This epithet denotes the pale stripe on the propleura of this species.

#### *Pseudoxenetus regalis* (Uhler)

*Xenetus regalis* Uhler, 1890:80.

*Xenetus scutellatus* Uhler, 1890:81. **New Synonymy.**

*Stenidea scutellata*: Townsend, 1891:54.

*Stenidea regalis*: Townsend, 1891:54.

*Pseudoxenetus regalis*: Reuter, 1909:67; Carvalho, 1958:150; Akingbohunge et al., 1972:12; Henry and Smith, 1979:215; Wheeler et al., 1983:142.

*Pseudoxenetus scutellatus*: Reuter, 1909:67; Carvalho, 1958:158; Akingbohunge et al., 1972:12; Henry and Smith, 1979:215; Wheeler et al., 1983:142; McPherson et al., 1983:37.

Uhler (1890) described *regalis* and *scutellatus* in Distant’s mirine genus *Xenetus*. Reuter (1909) recognized that the Uhler species were not congeneric with *lanuginosus* Distant, the type-species of *Xenetus*, and erected *Pseudoxenetus* to accommodate them. Van Duzee (1916) recognized *regalis* as the type of *Pseudoxenetus*.

Carvalho (1958) recorded *regalis* from New York to Michigan, south to Texas and Florida, whereas *scutellatus* is listed from Massachusetts to Minnesota, and south only to Missouri and North Carolina. More recently Akingbohunge et al. (1972) reported *regalis* from Wisconsin, and Henry and Smith (1979) recorded *scutellatus* from Georgia.

There is an obvious gradation from north to south, with the dark-color form *scutellatus* more common in the north and *regalis* with the orange pronotum more common in the south. Blatchley (1926) is the only worker to suggest that *scutellatus* might be a color form of *regalis*.

I have studied a series of both color forms taken in North Carolina, near Charlotte (by A. G. Wheeler, Jr., PDA), that were collected as nymphs (and reared) and adults on the same trees and dates. My initial examination revealed only the striking orange-color difference of the pronotum in *regalis*, the only character used to separate the two forms in several keys (Blatchley, 1926; Knight, 1941; Froeschner, 1949).

In addition, I found by taking 4 males and 4 females from the North Carolina series that measurements of the various body structures (head, rostrum, antennae, and pronotum), do not vary by more than 0.10 mm and often overlap. Male genitalia were examined and they, likewise, show virtually no variation between the two forms. In fact, the male parameres are nearly identical. This is particularly significant in the tribe Orthotylini where male genital structures are especially distinct for many species. Kelton (1959) illustrated the parameres and aedeagus of the dark-color form *scutellatus*.

Even though *regalis* and *scutellatus* appear morphologically inseparable, Uhler's (1890) original descriptions of the two are written quite differently, giving the impression to a casual reader that, as species, they are distinct in general body form and pubescence. After close examination, however, it is clear that both will fit either description with only a mere modification of the pronotal coloration.

Further, simple red-black color dimorphism is documented for other taxa. Carvalho and Schaffner (1975) treated a similar case when they considered *Barberiella apicalis* Knight (known from the northern U.S.) a junior synonym of *B. formicoides* Poppius (known from Texas). They showed that other than the reddish-brown color of *formicoides* and the black color of *apicalis*, the two mirids showed "no consistent differences in the external characters or morphology of the genitalia." Naito (1983) found that the rose sawfly, *Arge nigrinodosa* (Motschulsky), exhibits a red-black dimorphism on the mesepisternum of the thorax. Populations in northern Japan have the mesepisternum black, while several more-southern populations have this structure red. He showed that the color dimorphism in *nigrinodosa* was "... controlled by a simple Mendelian system—a simple-locus two-allele system—where the red allele is dominant over the black one," and proposed "that the red allele was derived from the black as a dominant mutant."

For the reasons discussed above, I consider *regalis* and *scutellatus* conspecific color forms. Because *regalis* has been designated as the type of the genus (and has page priority), it is the name that should be used for the species.

For nomenclatural stability the following lectotypes in the USNM are designated for *regalis* and *scutellatus*.

*Pseudoxenetes regalis*.—Female lectotype: Label 1, "Tex."; 2, "*Stenidea regalis*



Uhler" (handwritten); 3, "Type No. 1138, U.S.N.M."; 4 (here added), "Lectotype: ♀, *Xenetus regalis* Uhler, by T. J. Henry" (USNM type No. above retained). This specimen, having Uhler's handwritten identification label, appears to be one of the specimens he mentioned from Texas and is considered part of the original syntype series.

*Pseudoxenetus scutellatus*.—Female lectotype: Label 1, "N. Ill."; 2, "28"; 3, "Straumbg." (handwritten); 4, "P. R. Uhler Collection"; 5, "Lectotype: ♀, *Xenetus scutellatus* Uhler, by T. J. Henry (USNM No. 100945)." This specimen is selected as the lectotype instead of a specimen found in the USNM type collection (with type No. 1137) from "C. Mo." Uhler stated that *scutellatus* was common in Illinois but did not mention Missouri in his original description; therefore, the Missouri specimen cannot be considered part of the original syntype series.

*Ranzovius clavicornis* (Knight)

*Psallus clavicornis* Knight, 1927a:13; Blatchley, 1928:20.

*Excentricus mexicanus*: Blatchley, 1926:962 (in part); Blatchley, 1928:17.

*Ranzovius contubernalis* Henry, 1984:61; Wheeler and McCaffrey, 1984:68. **New Synonymy.**

*Ranzovius* (= *Exocentricus* [sic]) *clavicornis*: Mead, 1984:2.

Knight (1927a) described *clavicornis* based on a specimen collected at Drury, Maryland (near the Patuxent River) taken on *Pinus virginiana* Mill. (Pinaceae), and two at Washington, D.C., found feeding on mealybugs. Other than Blatchley's (1928) listing, no other mention of this species has appeared in the literature.

Recently, in a revision of the spider-web inhabiting bugs of the genus *Ranzovius* (Henry, 1984), I described the species *contubernalis*, based on a large number of specimens from Connecticut, District of Columbia, Florida, Maryland, North Carolina, and Virginia. Wheeler and McCaffrey (1984) presented an interesting companion study on the life history and behavior of *contubernalis* and described the fifth-instar nymph.

While preparing for the revision of *Ranzovius*, I discovered that a specimen in the USNM labeled as the holotype of "*Psallus varicornis* Knight" was conspecific with the species I was describing as *contubernalis*. Eventually, however, I was able to confirm that the epithet "varicornis" was only a manuscript name. This prompted me to include the specimen as a paratype of *contubernalis*.

After my revision of *Ranzovius*, I came across the description of the species *Psallus clavicornis*, described from Drury, Maryland. Not being familiar with this species, I consulted the USNM type collection to examine the holotype. In place of the holotype was a note reading "Not located, Apr. 82" (by R. C. Froeschner, USNM). After studying the original description of *clavicornis* and comparing the label data of the Drury specimen, I was able to piece together that the holotype of *clavicornis* was mislabeled by Knight as "varicornis." Further search of the Knight collection (USNM) revealed the two other specimens Knight (1927a) chose as paratypes for *clavicornis*, but as with the holotype, they were labeled as "varicornis." Apparently in preparing for publication, Knight decided on a different name for his species, but never relabeled his types. It is now clear that *Ranzovius contubernalis* is a junior synonym of *Psallus clavicornis*.

The combination *R. (=Excentricus) clavicornis* was published ahead of the above explanation (Mead, 1984) based on an identification by me of a single specimen collected in Florida. It should be noted that *Excentricus*, listed as a synonym in that report, is a valid generic name and is not congeneric with *Ranzovius*, although it has been used in combination with several species of the genus (see Henry, 1984).

*Saileria compsus* (Reuter), **New Combination**<sup>1</sup>

*Orthotylus compsus* Reuter, 1907:14; Van Duzee, 1907:29; Knight, 1927b:181.

*Orthotylus compsus* was described from a single specimen taken at Kingston, Jamaica (Reuter, 1907); Van Duzee (1907) gave this same record in his list of the Hemiptera taken on Jamaica. The only other record for this species was given by Knight (1927b) from Helotes, Bexar Co., Texas.

I have studied the holotype of *compsus* (CAS), the three specimens collected by Knight (USNM), and two additional males (USNM) taken by N. L. N. Krauss on *Lantana camara* L. (Verbenaceae) at Kingston, Jamaica in December 1955; and find that this orthotyline belongs in the genus *Saileria* Hsiao. Although the Knight specimens are females, the shorter second antennal segment of one specimen (antennae missing on other specimens) suggests that they are correctly associated with the species *compsus*.

Species of the genus *Saileria* are very similar in having a pale translucent dorsum sprinkled with green blotches or spots. *Saileria compsus* appears closest to *S. irrorata* Henry in color pattern and male genitalia. This species will run to couplet 3 in my key (Henry, 1976) with *bella* Van Duzee and *irrorata*. It can be separated from *bella* by the small round spots on the dorsum, compared to the large quadrate blotches on *bella*. From *irrorata* it is distinguished by the shorter second antennal segment that is about  $\frac{3}{4}$  the length of that in *irrorata* (*compsus*: 0.72 mm for males, 0.70–0.74 mm for females; *irrorata*: 0.94–1.00 mm for males, 0.92–0.98 mm for females). Also, the primary spiculum of the male aedeagus is hooked with the apical area serrate, compared to the broadly rounded and smooth apex of this structure on *irrorata* (figured by Henry, 1980).

*Taylorilygus pallidulus* (Blanchard)

*Phytocoris pallidulus* Blanchard, 1852:183.

*Lygus apicalis* Fieber, 1861:275 (synonymized by Carvalho, 1959:265).

*Lygus olivaceus* var. *viridiusculus* Knight, 1917:600. **New Synonymy.**

*Lygus pallidulus*: Carvalho, 1952:185.

*Lygus fasciatus* var. *viridiusculus*: Blatchley, 1926:762 (*lapsus*; incorrect species-sub-species association).

*Dagbertus olivaceus* var. *viridiusculus*: Kelton, 1955:284.

*Taylorilygus pallidulus*: Carvalho, 1959:265.

*Taylorilygus pallidulus* is a common, wide-ranging, weed-feeding species known from many parts of the world, including Africa, Asia, Europe, South America, and

<sup>1</sup> While this paper was in press I discovered that Carvalho (1976, Rev. Brasil. Biol., 36:57) previously recognized that *compsus* belonged to the genus *Saileria*.

North America (Carvalho, 1959). Snodgrass et al. (1984) provided an extensive list of host plants collected in Arkansas, Louisiana, and Mississippi. In many areas of the southern United States, *Conyza* [*Erigeron*] *canadensis* (L.) Cronq. (Asteraceae) is the favored host. For many years, this species went under the name of a junior synonym, *Lygus apicalis* Fieber. Kelton (1955) raised Leston's (1952) subgenus *Taylorilygus* to accommodate the *apicalis-simonyi* group of *Lygus* species. Carvalho (1959), who studied the type of *pallidulus*, recognized it as the senior synonym of *apicalis*. *Taylorilygus pallidulus* can be identified (as *Lygus apicalis*) using keys provided by Blatchley (1926) and Knight (1941).

Knight (1917) described *Lygus olivaceus* var. *viridiusculus* from Tisbury, Massachusetts based on two females. This variety has been discussed by Blatchley (1926), who considered it and the species *Lygus olivaceus* Reuter synonyms of *Lygus fasciatus* Reuter. Kelton (1955) correctly transferred *fasciatus* and *olivaceus* to the genus *Dagbertus* Distant but did not specifically mention *viridiusculus*. Leston (1979) clarified the status of the U.S. species of *Dagbertus* but was unable to place Knight's variety *viridiusculus*.

I have examined Knight's holotype (CU) and the paratype female (CAS) from Tisbury (dated 5-VIII) and find that both specimens are examples of *Taylorilygus pallidulus*, not a variety of either *fasciatus* or *olivaceus*.

In addition to the two type specimens, I have examined three males (CAS) determined by Knight, two as *Lygus olivaceus* and one as *Lygus fasciatus viridiusculus*. All three (2 from Tisbury, dated 25-VII and 6-VIII, and 1 from Manomet, MA, dated 8-VIII-1912) are *fasciatus*. The one specimen labeled as *L. fasciatus viridiusculus* probably indicates a *lapsus* on Knight's part, since he never published that combination, and also may have helped to develop Blatchley's (1926) concept of the subspecies. The study of these specimens indicates that Knight incorrectly recognized the species *fasciatus* and *olivaceus* (see discussion of *Dagbertus fasciatus* and *olivaceus*).

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## NOTES AND COMMENTS

### SURFACE VIBRATIONAL CUES IN THE PRECOPULATORY BEHAVIOR OF WHIRLIGIG BEETLES

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The surface film of a body of water is much like a thin elastic membrane stretched out at the air-water interface. The physical properties of this film are responsible for water occurring in discrete drops of dew, and on larger bodies of water the surface film can support the weight of a small animal such as an insect.

The unique habitat offered by the surface film of bodies of fresh water has been occupied by relatively few invertebrates. While many insects must periodically penetrate the surface film from below to breathe or above to oviposit, permanent residents are limited to a few families of water-striding or back-swimming Hemiptera, and to the whirligig beetles (family Gyrinidae) among the Coleoptera. A few spiders, such as *Dolomedes triton* also occupy this habitat (Bleckmann and Rovner, 1984; Bleckmann and Barth, 1984). For general information about whirligig ecology, see Hatch (1925), and Kolmes (1983b).

Members of both the water-striding and back-swimming families of Hemiptera and the whirligig beetles possess specialized sensory structures enabling them to detect minute vibrational stimuli in the surface film (see Murphey, 1971a and 1971b for a discussion of *Gerris remigis*; see Murphey, 1973 and Murphey and Mendenhall, 1973 for a discussion of *Notonecta undulata*). The use of surface vibrations as precopulatory signals has been demonstrated in both *Rhagadotarsus* (Wilcox, 1972) and *Gerris remigis* (Wilcox, 1979) and is strongly suspected in *Corixa* species (Thiess, 1982) all of which live at the air-water interface. I report an investigation of the precopulatory behavior of the whirligig beetle *Dineutes discolor*, done in order to see if vibrational stimuli are utilized by these animals as well. Whirligig beetles are only distantly related to Hemiptera, but I suspected that a convergence in communicatory systems might well exist due to the animals in question occupying the same rather unusual habitat. Certain of the precopulatory behavior patterns that I have reported earlier (see descriptions of *proleg-up* and *male mounting of female beetles* in Kolmes, 1983a) appeared to be likely candidates for signals involving a surface vibrational component.

The surface vibration detectors of whirligig beetles reside in their antennae. The antennae of whirligigs are unusually shaped with a club-like antennal flagellum arising from a flattened antennal pedicel that rests on the surface film (Kolmes, 1983b). The juncture between these two antennal regions is elastic, and sensory cells detect relative movement between the flagellum and pedicel (Wilde, 1941). These sensory units, the Johnston's organs, are extremely sensitive. In some species of whirligig beetle the Johnston's organs can detect vibrations of the surface film with an amplitude of only a few microns (Rudolph, 1967).

My strategy in this experiment was simply to take whirligigs who had already demonstrated their ability to carry out precopulatory behavior leading to copulation

in the laboratory, and to remove their antennal flagellae, thereby rendering their Johnston's organs inoperative. The removal of the antennal flagellae could be rapidly carried out on beetles anaesthetized with CO<sub>2</sub>, and no gross changes in the noncommunicatory behavior or survival of these animals resulted from this procedure. Experimental beetles continued to capture live *Drosophila* using their close circling behavior pattern (Kolmes, 1983b), and displayed all of the fifteen behavior patterns comprising my behavioral categories for *D. discolor* (Kolmes, 1983a). The beetles were housed in my laboratory individually in 1-liter aquaria, and their precopulatory behavior was observed by placing 2 male and 2 female beetles in a large observation aquarium. The beetles were collected from the Wisconsin River near Arena (Iowa Co.), Wisconsin. They were maintained in the laboratory on a diet of live flightless *Drosophila*. See Kolmes (1983a, b) for more details of my techniques for housing *Dineutes* in the laboratory.

Before these whirligigs had their antennal flagellae removed, I observed 15 copulations during 32 observation periods. Since there were 2 male and 2 female beetles present during each trial, I expressed this for analysis as 15 copulations for 64 pairs. After the beetles were deprived of their Johnston's organs, 10 observation periods resulted in no copulations. I expressed this for analysis as 0 copulations per 20 pairs. Comparing these data using a  $\chi^2$  2  $\times$  2 contingency test (see Siegel, 1956 for details) the difference between the behavior of the animals with and without their surface vibration detectors differs reliably at  $P < 0.05$  ( $\chi^2 = 4.42$ , df = 1).

Removing the antennal flagellae of a gyridid severs the three bundles of scolopidia making up each Johnston's organ (Wilde, 1941). These scolopidia produce the synchronous sum potential Rudolph (1967) found when electrophysiologically monitoring the antennal nerves of beetles subjected to surface vibrations. The removal of antennal flagellae therefore destroys the surface vibrational sensitivity mediated by gyridid Johnston's organs. Could this removal interfere with the reception of signals conveyed by other sensory systems?

Tactile hairs are the only sense organs revealed by a scanning electron microscope examination of whirligig antennal pedicels, and these hairs continue to contribute sensory input used in predatory behavior after removal of antennal flagellae (Kolmes, 1983b). No sensory systems other than those of the Johnston's organs have been described from gyridid antennal flagellae (Wilde, 1941; Rudolph, 1967) and any other sense organs present must be quite inconspicuous compared to the antennal specializations for mate detection found in many male insects.

It is likely that several sensory modalities are involved in whirligig precopulatory behavior. Whirligigs have well developed vision (Bennett, 1967; Brown and Hatch, 1929; Carthy and Goodman, 1964) and some of the potential precopulatory signals previously identified (Kolmes, 1983a) likely possess visual components. Gyridids are morphologically a very uniform group, and multispecific swarms have been described (Heinrich and Vogt, 1980). This may provide the impetus for chemically mediated species recognition cues, with male precopulatory mountings of female beetles providing a possible interaction during which contact chemoreception could occur (Kolmes, 1983a). Further experiments will be required before the contributions of signals conveyed through all of the sensory modalities of *D. discolor* can be clarified.

Clearly the main point of interest to arise from this experiment is that *Dineutes*

*discolor* do rely on surface vibrational sensitivity in their precopulatory behavior. My data are not adequate to point out precisely what signals my procedure interfered with, however two behavior patterns that might be involved are female proleg-up and male mountings of female beetles (Kolmes, 1983a). Both the Hemiptera specialized for life on the surface film, and whirligig beetles, have come to utilize this elastic membrane as a channel for transmitting vibratory signals.

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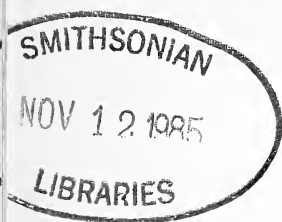
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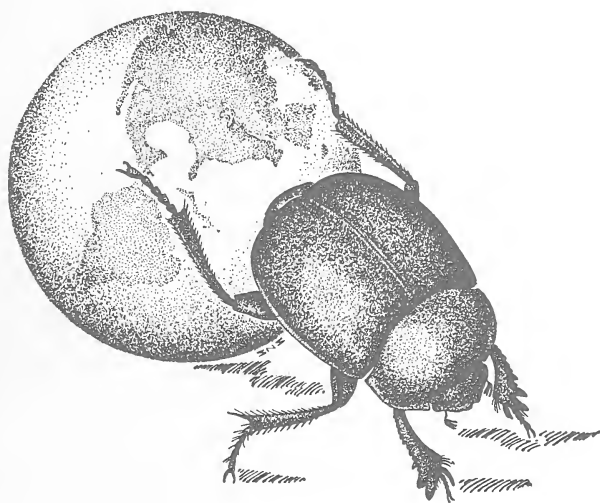
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**CHARLES P. ALEXANDER: A TRIBUTE, WITH EMPHASIS  
ON HIS BOYHOOD IN FULTON COUNTY, NEW YORK,  
AND HIS STUDIES AT CORNELL UNIVERSITY**

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Charles Paul Alexander died nearly four years ago, but entomology will not forget "Doc Alex." The sheer numbers of his taxonomic accomplishments will not allow it: the description of some 11,000 species of flies in more than 1,000 publications. He dedicated his life to making better known a family of Diptera he found fascinating, the crane flies or Tipulidae. His prolific output of species descriptions, particularly the naming of more than 10,000 species in a single family, most likely will never be surpassed.

But Professor Alexander was more than an outstanding taxonomist. He was a well-rounded student of natural history; an enthusiastic teacher who introduced the basics of entomology to an estimated 4,000 students at the University of Massachusetts, Amherst; an administrator, who at Amherst served as chairman of the Department of Entomology and Zoology and as dean of the School of Science; and an active member of several scientific societies and a past president of the Entomological Society of America.

Many of Dr. Alexander's friends and students—*family* to "C. P." and his wife Mabel—will remember the warmth and affection they found on visits to "Crane Fly Haven," his home laboratory at 39 Old Town Road, Amherst. The letters I received from Dr. Alexander during 1977-1980 reveal a willingness to praise others' work, or as J. C. Bradley put it, a way of making "a fellow feel that he has amounted to something in this world" (1). Wielopolska (1978) simply, yet elegantly, captured his personality by saying he was "a person of great charm."

Alexander's achievements are so remarkable as to seem incredible, considering that he made nearly all his own illustrations (about 15,000) and worked without the aid of large government grants or technical assistance (except for his wife). His distinguished career deserves the informative accounts that Ashley B. Gurney (1959) and George W. Byers (1982) have provided. More can be written about his life and work, but I am not a dipterist, and therefore one who might be qualified to evaluate his contributions to tipulid systematics or his concepts of intraspecific variation, nor a colleague who can capture the essence of his personality; indeed, I never met him. We did, however, share a fondness for Cornell University. A few years before his death, I encouraged Dr. Alexander to publish his Cornell experiences and association with John Henry Comstock's legendary department, but his wife's death in 1979 and his own failing health kept him from preparing such a paper. I hope I am not presumptuous in inferring from his letters a desire for someone to detail his early years, especially his "wonderful Cornell days" (2).

## UNCONVENTIONAL CHILDHOOD: AN ADIRONDACK NATURALIST

Charles Paul Alexander, born at home on Poole Avenue, Gloversville, New York, September 25, 1889, was the youngest child of Emil and Janet (Parker) Alexander. His father, of Polish descent and born in Berlin on December 3, 1852, was christened August Emil Schladensky (3); his mother was born August 19, 1851, in Johnstown, New York (4). Mr. Alexander came to the United States from Germany in 1873. A skilled worker with leather, he settled in Johnstown to work in the glove industry of Fulton County, adopting the name Ernest August Emil Sladensky. In 1874 he had his name legally changed to Emil Alexander. The family name was difficult to spell and pronounce (5), and he also wanted to avoid the embarrassment of being continually confused with an unsavory town character having a surname that sounded too much like "Sladensky" (6).

When Charles was only a year old, his parents' house was destroyed by fire, and the Alexanders moved to Woodside Avenue near Gloversville's south end. The family had little money and no luxuries, but Charles enjoyed "an ordinary childhood" with "wonderful parents and good friends" (7). For two years beginning at age 10 he sold newspapers on the street, making relatively large sums (\$4.00–5.00) in 1901 upon the deaths of Queen Victoria and President McKinley (8).

*Maps, birds, and plants.* The young boy (Fig. 1), Chuck or Chuckie as he was known to his friends, found maps particularly fascinating (9). This early preoccupation led to a keen appreciation of geography, which later would aid his worldwide studies of crane flies. Although he never travelled outside North America, Alexander usually enhanced his regional works on tipulids with introductory "comments on the topography, climate, vegetation and other geographic aspects of the area concerned" (Byers, 1982). As Gurney (1982) noted, he "read so broadly on foreign areas that he could visualize conditions of particular regions and their zoogeographic relationships to other foreign areas."

From earliest youth animals provided another source of pleasure. He filed pictures of animals cut from magazines and comics and spent hours observing wildlife in the unspoiled country near his home. With his friend Axel Olsson he explored Simmons Woods and its "clear sparkling brook." Wild flowers, birds, and insects came under their scrutiny. They maintained a list of Fulton County plants; particularly exciting finds included the seldom-seen ginseng that the boys discovered on the slopes of Bleeker mountain above the Gloversville reservoir, and the little orchid *Listera australis* they found growing on sands above Olsson's home on Park Street (10). Somewhat later came camping trips to mountains, ponds, and lakes (Caroga, Canada, and Mountain) of the southern Adirondacks. They also explored the Sacandaga River, its Sport Island, and the nearby vast marshland known as Vlei (11).

Clearly the boys viewed nature differently from their schoolmates. Avoiding (or maybe lacking time for) baseball and other kids' games brought scorn from neighbors and relatives who predicted the two "would never amount to much" (12). Some 60 years later Alexander suggested to Olsson that the negative feelings about their scientific endeavors, especially from the latter's cousin Albert, were inspired by envy (13). This seems reasonable considering all that Alexander accomplished before graduating from high school.

At about 10 years of age Alexander had become interested in birds. He kept a



Fig. 1. Chuck Alexander at 11 years of age (courtesy of Smithsonian Institution Archives).

notebook of Fulton County species, which contained descriptions and key recognition features, detailed notes on their habits and songs, line drawings, and a few water color illustrations (14). A short article, entitled "A Young Woodcock," appeared in the March 1903 issue of *American Ornithology* when he was only thirteen. This article reported his discovery of a woodcock and her four young. Charles wrote about

picking up one of the little birds: "I wanted to take it home but it cried so sadly and pitifully that I put it down and continued on my way" (Alexander, 1903). Between 1904 and 1910 he published fifteen additional notes on birds and their eggs, all in *The Oologist* (15). In responding to a reader's criticism of his observations (Alexander, 1905) or answering an editor's query regarding the identity of a species he observed (Alexander, 1908a), Charles demonstrated a good knowledge of birds and the ornithological literature. It may be said that some of his bird studies seem trivial, but the articles were generally well written. His observations of a nighthawk reveal an interesting, anecdotal style: "Once in a while the birds come and alight in the tall pine trees studding the blue-berry fields and so lethargic are its slumbers when thus alit that a stone may be thrown that hits the branch upon which the sleeper sits, and still he 'waketh not'" (Alexander, 1904).

During his senior year (1906), Charles' deep commitment to birds was revealed by his copying much of Gould's *Birds of Australia*, discovered at Lenox Library on a visit to his brother Will in New York City. While in charge of surveying Fulton County for E. H. Eaton's *Birds of New York* (see Eaton, 1910 for acknowledgment of Alexander's data), he so neglected his studies to observe the spring migrations that he nearly failed his courses, especially German (16).

How did young Alexander develop such an intense interest in natural history? Was it an innate curiosity about living things, perhaps reinforced by Axel Olsson's companionship and similar leanings? He admitted that they were the only true naturalists in their families; each had an older brother interested mainly in music or poetry and an older sister who was a housewife (17). On a field trip with his brother William, Charles referred to himself as the "scientific man" of the expedition (Alexander, 1908b). William was to become a prominent naturalist and conservationist (18), but his biological interests appear to have developed after his younger brother's formative years (19). Furthermore, William was in Germany studying music during a five-year period when Charles was active in his bird work (20). His father may have had some influence, for Charles characterized him as having "a keen love and appreciation of nature" (21). As a boy, Charles' father had made an insect collection in Germany (22). A biology teacher in the Gloversville schools also may have been influential (23). Alexander, however, seemed to credit his mother for his biological bent: "Unquestionably most of what I am or can be is due to her" (24).

#### TURNING TO INSECTS, DISCOVERING "TIPS"

Although Alexander continued his bird studies by following the 1908 and 1909 spring migrations for W. W. Cooke of the U.S. Biological Survey (25), he had realized by winter 1906 that "the field of local bird study was becoming restricted" (26). He also knew that there were only about 20,000 species of birds in the world compared to almost that many insects in New York or New England (27). He began collecting insects in earnest, making for each capture a detailed entry in his journals, and soon accumulated a considerable collection. During trips to Albany in connection with his bird studies (1904–1905), Alexander had met State Entomologist E. P. Felt and his assistant, D. B. Young. On another trip to Albany he stopped at Felt's office on State Street below the Capitol and obtained identifications for some of his specimens. Gradually, through correspondence, he became acquainted with other leading spe-



cialists—Nathan Banks, C. W. Johnson, J. G. Needham, E. A. Schwarz, and E. P. Van Duzee—who provided identifications of insects in various orders (28).

An interest in collecting almost all kinds of insects, especially Odonata and other aquatic forms, soon led to a fascination with some longlegged flies encountered in Simmons Woods and elsewhere. Alexander had no idea what these insects were—crane flies (Tipulidae), or “tips” as he would fondly call them in later life—or that they would be the subject of his life’s work. “I saved all these flies that I could find and by June had a small box with twenty or thirty pinned individuals” (29).

In late June 1906 he again stopped in Albany on his way to visit his brother, hoping such a well-trained entomologist as Dr. Felt could easily identify the long-legged flies. About that eventful meeting he wrote: “Without seeing the contents, he replied that he would be glad to name all he could. I can recall the sinking feeling that came over me when he opened the box and upon seeing that they were all crane-flies said ‘I’m sorry that I cannot help you, but there is no one in this country who can name these flies’” (30). “But wait,” said Felt, “here is one I can name.” Alexander grabbed his notebook to record *Bittacomorpha clavipes* (F.), a phantom crane fly, species number one in what “was destined to become the greatest single collection of these flies ever amassed” (31).

After getting over his initial disappointment, Alexander was able to appreciate the significance of Felt’s remarks. If an entomologist of his experience was unaware of anyone who could identify North American crane flies, then they would serve as an ideal group for investigation. He decided to spend the remainder of his life studying tipulids (32).

*Of college caliber.* During a visit with Dr. Felt in spring 1907, Alexander was, in his words, hit by a “bombshell.” The State Entomologist “galvanized me when he remarked that no matter what hardships it might entail, he advised me to go to College and continue the study of insects. I was then a senior in the Gloversville High School and this was absolutely the first idea I had that I was possibly of college calibre. In these early days, it was a rare event for a boy or girl to ‘go to college’” (33).

Felt specifically recommended Cornell University at Ithaca, New York, where J. H. Comstock had assembled an outstanding faculty in entomology. That Cornell was the place to go for entomological training was reinforced by Alexander’s acquaintance with James G. Needham. In 1906 Charles had collected an unusual mayfly on Sport Island in the Sacandaga River. The specimen, a single female (Alexander later provided specimens of both sexes), was given to Felt, who forwarded it to Needham, then at Lake Forest College in Illinois (34). Needham, recognizing that the mayfly’s remarkably developed abdomen showed affinity only with a New Zealand species, described a new genus and species, *Siphonisca aerodromia* (Needham, 1909). Even today, Alexander and G. C. Crampton are thought to be the only entomologists who have seen a living specimen of this rare, interesting species (Edmunds et al., 1976). Alexander had been intrigued with Needham’s (1908) report on crane flies of Old Forge, New York, in the Adirondacks and had corresponded with him during 1906–1907. He later acknowledged that it was Needham’s letters and “kindly advice” that were instrumental in his continuing devotion to these insects. After Needham accepted a limnology appointment at Cornell in February 1907, Charles decided he would like to be his student (35).



Following graduation from high school in 1907, Alexander applied for fall admission to Cornell but was denied because he lacked German III. By then it was too late to make up the deficiency with a post-graduate course. When the Alexander family moved to nearby Johnstown in July (36), Charles began working in a glove factory, earning \$1.00 for a 10-hour day. The next year he was allowed an hour a day to take German III at Johnstown High School. In June 1909, having met Cornell's requirement of three years of a modern foreign language, he was accepted for the fall term (37).

Working 10 hours a day for two years did not keep Alexander from collecting "vast numbers of insects" (38) (Fig. 2) and accumulating about 1,500 determined species by summer 1909 (39). Before nightfall he would collect at a nearby cemetery and along Hales Creek, then would return home for supper. Apparently Charles' mother not only put up with having to fix late meals but encouraged her son's work: "A mother who believed in me and appreciated to the full what this meant to my future life, made this course possible" (40).

During this period, Alexander devoted some attention to beetles, often taking an insect net along on birding expeditions (Alexander, 1908b). Among Coleoptera, he emphasized staphylinids and obtained identifications from Felt and E. A. Schwarz; this group, not the Tipulidae, was the subject of his first entomological paper. Notes on rove beetles of eastern New York appeared in the February 1909 issue of *Philatelic West* and continued in the May and July numbers for that year (Alexander, 1909). Alexander did not list this obscure paper in the compilation of his writings (paper number 685 in Oosterbroek and Theowald, 1980), and because it was not recorded in *Zoological Record*, this paper probably has gone unnoticed by coleopterists.

But young Alexander spent most of his time collecting Tipulidae, which were sent for determination to C. W. Johnson of Boston. This material contained "several striking new species" and "many rarities" (41). Johnson (1912) named one of Charles' tipulids *Elliptera* (now *Gonomyia*) *alexanderi*, the first of many species dedicated to him. Receiving names for many of the Fulton County specimens gave him his "first appreciation of the richness of the Tipulid fauna of the southern Adirondacks and also . . . that very many species . . . awaited discovery and description." Johnson's gift of volume 4 of Osten Sacken's monograph of North American Diptera (Osten Sacken, 1869), shortly before he left for Cornell University, enabled him to have "a fair idea of the size and importance of the group" (42).

His first paper on crane flies (Alexander, 1910) was based on collections made in Fulton County the summer before he entered college. From May to September 1909 he traversed the county, often collecting until sundown and once persisting through a rainstorm to secure a specimen. Alexander's first new genus was *Sacandaga* (Alexander, 1911), named for the river and proposed to accommodate the species *flava*, which he collected on Sport Island as early as June of that year (43).

#### CORNELL DAYS: THE GOLDEN AGE

Alexander had managed to save about \$500 from working in the glove factory at Johnstown, but he entered Cornell "terribly poor" (44). Arriving in Ithaca on September 23, 1909, two days before his twentieth birthday, he found suitable (and probably inexpensive) quarters in the home of Professor Robert Lee Shipman on Dryden Road near the south entrance to campus (45). Though he cooked most of

Part I.

Plants of Insects.



Aquatic; root stalks, long, cylindric, horizontal and thick; leaves cordate and large; flower yellow.

Look for this species in the muddy sloughs along streams, and especially in H. Vanderburg's Pond. *Doracia palmata* should occur; also *D. cincticornis* (N. Hamp.)

*Galerucella nymphaea* - is to be looked for especially.

Fig. 2. Page from one of Alexander's diaries and notebooks; this one, from "Entomologia, Reference Book, (Field) 1907," shows his attention to plants as hosts of particular insects, in this case Chrysomelidae (courtesy of Smithsonian Institution Archives).

his meals at Shipmans to save money, he found his savings melting rapidly. Soon came an opportunity to tend two home furnaces, with one of them paying his room and the other, with an occasional third, providing some spending money (46). For a time, he also worked from 2 to 7 A.M. for an ice company located near the southern end of Cayuga Lake (47). He was able to earn additional money by working in the entomological library for Professors A. D. MacGillivray and W. A. Riley (48). He genuinely appreciated the assistance from Cornell's entomology faculty: "From the very first Comstock, Needham, and almost all the others seemed to go out of their way to be good to me and to help in various ways" (49). One reason for the good early impression he made on Comstock and MacGillivray was his arriving with five specimens of the primitive dipteran *Protoplasma fitchii* Osten Sacken (Tanyderidae), then considered "incredibly rare" (50).

On his second day in Ithaca, Charles was eager to explore the campus—to find "sanctum sanctorum," the Entomology Department, housed on the upper floors of Roberts Hall, which would be "home" for the next eight years (51). He located the building on Cornell's agriculture campus and was browsing in the entomology library, "marvelling at the vast number of books and pamphlets there available" (52), when he was approached by a fellow freshman who mistook him for an advanced student. "Sir, could you tell me where I could find a copy of Aldrich's [1905] Catalogue of North American Diptera" (53)? The other student was Mortimer D. Leonard, who had arrived in town the night before. Locating the volume, the two admired its contents and discussed a mutual interest in dipterology. Thus was born a deep, life-long friendship with Mort, who was to stay at Cornell for a Ph.D. in entomology and to gain prominence for editing the New York insect list (Leonard, 1928), publishing numerous papers on insect biology and distribution, and becoming one of the first well-trained entomologists to serve industry (see Wheeler, 1978). Alexander cherished his friendship with Leonard, several times writing Mort on September 24 to commemorate their fortuitous first encounter, which he termed "a most fortunate circumstance" (54). To Leonard and his wife Doris he wrote in 1959: "I am writing this letter on the above date specifically and intentionally since according to my firm belief it was exactly fifty years ago today that Mort and I had our historic meeting in Roberts Hall. I, too, have told of this initial meeting to many people and it is most certainly one of my fondest recollections" (55).

The two freshmen then left the library to see if they could get a glimpse of Professors Needham or Comstock—"great names to youngsters about to be initiated into the vast world of entomology" (56). Next to a pillar in Roberts they spied a tall, well-dressed man who surely had to be Dr. Needham. At this same time a "vigorous man of middle age, with a bucket in one hand," came up the stairs; this, they decided, must be the janitor. Shortly after, they discovered their error. The "aristocratic white collared gentleman" was the janitor; the other proved to be Dr. Needham, who was returning from field work at the nearby Renwick Marsh (57).

*Undergraduate academics and employment.* In his freshman year Alexander took several "attractive" courses that increased his "knowledge of insects and the other subjects beyond all expectation" (58). One of the most exciting was Dr. Needham's General Biology, a new offering in fall 1909 that was required of all students in the

College of Agriculture. It was based on a textbook bearing the same name, which would appear the following year (Needham, 1910). This first year of the course students had to use page proofs of the book (59).

Although Alexander had corresponded with Needham as a high school student and had chosen Cornell specifically to study under him, he did not meet the Professor until General Biology had met for some two months. "I made no effort to foist myself upon him, since it was readily apparent that he was a very busy man." But one day "the 'Master' came up the aisle and paused beside the desk where I was working. After a moment' [*sic*] silence he said, in his profound voice, 'Is your name Alexander?' I admitted this fact, and it was followed by 'C. P. Alexander of Gloversville?' This, too, was admitted. 'Well, well, will you come into my office, please?' Upon doing this came a severe but gentle rebuff over not having made myself known to him earlier" (60).

The entomology faculty must have realized that this atypical freshman demonstrated exceptional potential. Soon after Alexander began his studies, Professor Comstock called him to his office to ask if he would like to become an active member of the Entomological Society of America, and he was proposed for election at the end of his freshman year (61). It also was during his first year at Cornell that he set as a life goal the description of 5,000 new species of Tipulidae (62).

That first year Needham scrutinized Alexander's work, and following the end of second semester he asked his protégé to spend the summer in Ithaca collecting material for succeeding years' biology classes. At the Department's Limnological Laboratory on Renwick Flats at the south end of Cayuga Lake, he accumulated frogs, crayfish, fruiting liverworts, and a multitude of other organisms necessary for teaching a class of about 500 students (63). The 20 cents an hour he received, "a princely sum in those days" (64), was double what he had made in Gloversville. At the end of his summer's work he wrote: "Today I left Ithaca for home after the most splendid summer of my existence. It passed like a dream" (65). In 1911 Needham again asked Alexander to stay for part of the summer to collect teaching material (66).

But the work of summer 1912 was to be Alexander's most memorable Cornell experience. Since spring he, Mort Leonard, and other students had been making plans to join Professor J. Chester Bradley on the Cornell Biological Expedition to Okefenokee Swamp in southern Georgia (Wheeler, 1978). One day, though, Needham asked Charles just how much his heart was set on making this trip; bravely, he replied "not too much" (67). The Professor then revealed that Liberty Hyde Bailey, Dean of the Agriculture College, had asked him to institute a course that would acquaint Cornell students with natural resources of the agriculture campus and associated university farms. For the new Farm Course, Needham was to remain in Ithaca for the summer to make preparations; he asked that Alexander stay to help him and to assist him with the course the following year. Thus, professor and student spent most of that summer building an outdoor amphitheater in Cascadilla Gorge near the athletic fields. It was difficult work: soil had to be dynamited and carried away to allow construction of a "series of stone seats arranged in concentric semicircles before a concrete pulpit" (68). Each morning, after they carried in a basket of dynamite, Alexander would tamp down the sticks—ticklish work, but he loved it. "This summer



with Dr. Needham was one of the most instructive in my whole life, since our daily conversation embraced about everything in the world of living things and there was no question I could ask that was not answered by the teacher" (69).

Alexander earned an additional \$400 for serving as an assistant in General Biology his junior year, and \$500 his senior year for assisting Mrs. Comstock in Nature Study and Needham in Limnology (70). For an undergraduate, serving as an assistant to several professors was an unusual experience. Other valuable training was obtained from courses taught by the Cornell faculty. In addition to Needham's General Biology there were botany classes under George Atkinson, L. H. Bailey, E. J. Durand, E. Laurence Palmer, W. W. Rowlee, William Trelease, and K. M. Wiegand; ichthyology with A. H. Wright; histology with S. H. Gage; and geology with A. C. Gill, G. D. Harris, and R. S. Tarr (71). Palmer's advanced course in field botany proved "relatively simple" because of the substantial work he and Axel Olsson had done on the Fulton County flora (72). Later, Professor Palmer recalled how difficult it was to keep up with the two (73) in studies of the local flora (74). From the distinguished faculty in entomology, at that time recognized as unsurpassed in the United States (75), Charles was able to take J. H. Comstock's courses before that great teacher retired in 1914 (76). He also felt privileged to be among J. C. Bradley's earliest students, though he found him a "very strict disciplinarian" (77).

Having completed requirements for the baccalaureate degree in 3½ years (78), Alexander graduated in January 1913 (Fig. 3). In his senior year he was elected to full membership in Sigma Xi, an honor normally accorded graduate students and faculty (79). As an undergraduate he had published nearly 30 papers, including two with his friend Mort Leonard (Alexander and Leonard, 1912a, b), and had begun to study tropical forms (e.g., Alexander, 1912a, b). Even as a freshman Alexander had planned studies on cranefly biology that would lead to a Ph.D. (80), and so "it was tacitly understood that I was to continue graduate work at Cornell . . . upon some problem in connection with the Tipulidae" (81).

Events of summer 1913, however, nearly led Alexander to leave Cornell. At Orono, Maine, O. A. Johannsen had resigned his position with the Agricultural Experiment Station to return to Cornell to relieve Needham of part of the work in biology. Dr. Edith Patch chose not to hire a faculty member immediately but to bring in various specialists as summer workers. She invited Alexander to study systematics and biology of crane flies; joining him were A. D. MacGillivray, then at the University of Illinois after leaving Cornell in 1911 (see Mallis, 1971), who would conduct research on sawfly larvae, and Ohio State's Herbert Osborn who would work on Cicadellidae. The orthopterist A. P. Morse spent part of the summer in Orono. At Morse's suggestion, Alexander and Osborn accompanied him and an Indian guide on a nearly week-long collecting trip to Mt. Katahdin. In Alexander's words, he "became greatly attached" to Dr. Osborn and considered doing his graduate work at Ohio State. An increase in salary and an appointment as Instructor for Needham's Farm Course induced him to remain at Cornell (82).

*The graduate years, 1913–1917* (Figs. 4, 5). When Alexander and his friend Axel Olsson both decided to stay at Cornell for graduate study, they moved to the basement of a house on East Seneca Street near the university's infirmary (83). Otherwise, Alexander's transition from undergraduate to graduate student probably required





Fig. 3. Alexander's senior picture, which appeared in the *Cornell 1913 Class Book* (courtesy of Department of Manuscripts and University Archives, Cornell University).







Fig. 5. Alexander (foreground, fourth from left) with Cornell students on a field trip to Coy Glen, October 1916; his brother William is in back row with vasculum (courtesy of Smithsonian Institution Archives).

little adjustment, although impending war brought anxiety: "We never knew from one day to the next whether we might be called into service" (84) (Fig. 6). For his doctoral thesis he decided to work on crane fly biology, his important study appearing as Cornell memoir 38 (Alexander, 1920). "This having to locate and rear the great numbers of life histories was very exacting but gave me a grasp of Tipulid biology that . . . helped me constantly over the years that followed" (85).

During this period he earned \$750 annually as Instructor in charge of field laboratory work for Needham's Farm Course. The textbook used, *The Natural History of the Farm* (Needham, 1913), includes one of Alexander's illustrations (p. 63). Assisting with the course's various sections were several students, including Ralph Curtis and Lawrence MacDaniels, who became distinguished faculty members in Cornell's College of Agriculture (86).

In spring 1917 Alexander took his oral examination so he could begin looking for

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Fig. 4. Alexander as a Cornell graduate student, 1914 (courtesy of Smithsonian Institution Archives).



Fig. 6. Alexander as a cadet in the Cornell army corps, 1910; see note 84 (courtesy of Smithsonian Institution Archives).

jobs in entomology which, at that time, he and other students "found were very difficult to obtain or almost non-existent" (87). Soon H. B. Hungerford offered him an Instructorship at the University of Kansas in Lawrence; Hungerford in 1916 had been granted a year's leave of absence from the Kansas faculty to pursue doctoral work at Cornell (Woodruff, 1956). Again forgoing a Cornell Biological Expedition, Alexander accepted the offer to teach courses in taxonomy and to be assistant curator of the insect collections. When he reported for work at Lawrence on July 1, 1917, he had completed all Ph.D. requirements except finishing his dissertation (88). His degree was awarded in 1918, and a thesis he submitted for a "minor problem" in botany also bears that date (Alexander, 1918).

*Clubs, fraternities, and summer fun.* With his coursework, assisting several professors, and publishing extensively on Tipulidae, one might wonder if Alexander found time to participate in campus affairs. Somehow he did. He was active in the Agassiz Club, founded about 1908 for undergraduates interested in biology (Wright, 1953). Members met weekly for presentations, either formal or of a more general nature, and for field excursions. He was president one year, and as secretary his senior year (89) he arranged the programs. He solicited talks from nearly every professor and capable graduate student and was grateful for their willingness to serve the club (90). For the spring semester of 1912 he was elected president of Jugatae (91), the oldest entomological society in American universities. Named after Comstock's discovery of the primary division of Lepidoptera into Jugatae and Frenatae, the society met weekly for entomological talks by faculty and advanced students (92). His first presentation to Jugatae, "Myrmecophilous Coleoptera," was made on May 16, 1910 (93). In June 1915 he was part of a team organized by Professor A. A. Allen for surveying birds of the central campus, part of a national effort coordinated by the U.S. Bureau of Biological Survey (Smith, 1984).

On a more social than scientific level Charles, with Harry H. Knight and others, was in 1914 a founder of the Zeta Chapter of Alpha Gamma Rho, a national agricultural fraternity. Alexander remarked that he and Knight, a graduate student studying plant bugs (Miridae) (see Wheeler, 1979), not only shared an interest in systematic entomology and the fraternity but also suffered financial hardship during their college careers. He delighted in listening to Harry's tales of hunting wild turkeys as a boy growing up in the Missouri Ozarks (94). Alexander also was a member of Helios, the senior agricultural society (95), and Gamma Alpha (96), a graduate scientific fraternity (Wright, 1964).

One of Alexander's most enjoyable events during his eight years in Ithaca was the "lamprey banquet" held at the inlet to Cayuga Lake (97). He also was a football fan. In a letter to J. C. Bradley in early November 1920 he said he "would especially like to be back to root at the ball-games" (98). On the eve of that year's annual Thanksgiving Day game with the University of Pennsylvania, he noted that he hoped Cornell "would lick Penn to a frazzle" (99).

There also were happy times spent as a member of "a little select group" known as Cynophilidae (or Gastrophilidae) (100). Charles, his brother Will (who had enrolled at Cornell in 1915 at age 33), Axel Olsson, Professor Needham's son John, and a few other graduate students would assemble at the Needhams to play cards, using matches for their bets. A good meal would follow: "'hot dogs' and other accompanying materials, that suggested the names for the group" (101).



Summer trips also provided fun. In 1914 he camped with Olsson on the Sacandaga River near Vlei country. They studied the "rich Transition flora" (102), discovering several rare species. Their graphic description of the area attracted the attention of State Botanist Homer D. House, who spent two days with them checking their botanical finds (103).

Alexander's most enjoyable trip with Olsson came as a member of the Second Expedition of the *Ecphora*, a launch belonging to geology professor Gilbert D. Harris and used previously in paleontological explorations. Axel had invited his friend to serve as "entomologist" for the party, which also consisted of three geology students. Leaving Ithaca through Cayuga Lake in early summer 1915, they continued through the Barge Canal and Mohawk River to the Hudson, down the river to New York Bay, across New Jersey via the Raritan Canal to the Delaware River at Trenton, and down the river to Delaware City and through a short canal into the Chesapeake Bay above Baltimore. After investigating the Bay and Potomac River, they continued to Norfolk, Virginia, south by canal through the Dismal Swamp in southern Virginia, and into the northernmost sounds of North Carolina. When the party reached New Bern at the mouth of the Neuse River, Alexander found among his accumulated mail a letter from W. L. McAtee of the U.S. Biological Survey, inviting him to survey aquatic plants along the South Carolina coast. After a briefing in Washington, he spent several weeks between Georgetown and Charleston gathering data to help explain the decline in wild fowl that feed on aquatic vegetation. His work took him west to Reelfoot Lake in northwestern Tennessee before he resumed his studies at Cornell (104).

*Meeting his future wife and co-worker.* Even more eventful in 1915 than the excursion of the *Ecphora* was meeting his future wife, Mabel Marguerite Miller. Born in Brookview (Rensselaer County), New York, July 29, 1894, she moved to Gloversville after completing training at Albany Business College. She was working as a secretary for the E. J. Wilkins Co., a manufacturer of purses and similar articles, when Charles met her while visiting his parents. He continued to see her when he had additional time off from his studies, and they became engaged in 1916 (Alexander, 1979). The significance of meeting Mabel—for his sense of well-being in later years and for his unrelenting productivity as an entomologist—cannot be overemphasized. She was to serve as a co-worker on Tipulidae, typing his letters and manuscripts, preparing an invaluable index to his books and papers on crane flies, and even coauthoring two important tipulid catalogs with her husband (Byers, 1982). Charles did not drive a car, and it was Mabel who was to be "pilot, companion, and fellow collector" (Gurney, 1959) on all their many trips to the western states, New England, Canada, and elsewhere. Fender (1951), in naming a new species of cantharid after Mabel, said of her husband: "Fortunate indeed is this man who managed to marry a humorist, cook, chauffeur, stenographer, proof reader and ardent supporter—all one individual." "C. P." himself was to admit: "I could never have accomplished half of what I did without her at my side" (105).

#### POST-CORNELL YEARS: A RECAPITULATION

At Lawrence, one of Alexander's first duties at the University was to conduct an insect survey of the western Kansas plains, with assistance from three graduate

students during the 4- to 5-week-trip (106). Soon he and Mabel decided to marry, and she came by train to Kansas City where he met her. Professor S. J. Hunter took them to Lawrence (107). Their simple ceremony, attended only by entomology professors Hunter, H. B. Hungerford, P. B. Lawson and their wives, was held in Lawrence on November 10, 1917. Because of his relatively low salary at the University, it was necessary for Mabel to begin work as a secretary for a major business in Lawrence. In 1919 S. A. Forbes of the Illinois Natural History Survey arrived, without advance notice, to ask if Alexander would be interested in a position with the Survey in Urbana. Forbes, who insisted on interviewing a potential employee's spouse, had a "nice talk" with the couple; he then offered Charles the position at \$1,000 more than his current salary, which the two accepted together (Alexander, 1979). Later Alexander told Hungerford: "There was very little incentive to slave one's life out in the top floor of the Dyche Museum during the hot days of summer at the munificent salary of \$100 per month" (108).

From spring 1919 to August 1922 Alexander had charge of the museum at the Illinois Natural History Survey, and Mabel worked as a secretary for State Entomologist W. P. Flint. In 1921 H. T. Fernald, head of the Entomology Department at Massachusetts Agricultural College (now University of Massachusetts), wrote to ask if he would be interested in an assistant professorship at the Amherst school, the duties to include teaching insect taxonomy, medical entomology, and other courses. Although the Alexanders were happy in Illinois, they decided to accept the offer, mainly because they would be much closer to their aging parents; his work would begin the following year on September 1 (Alexander, 1979). Before they left, a New Year's Day fire damaged their home and possessions and destroyed many Cornell items (109). Just as firemen were arriving, the attic crashed down on Mabel, and she suffered severe burns before being pulled to safety. The Flints cared for her in their home during her month's convalescence (Alexander, 1979) (110).

Nearly throughout his tenure at Amherst, Alexander worked a seven-day week, squeezing in species descriptions between classes (111), and kept a nine-month appointment so he and Mabel could take summer collecting trips (Alexander, 1979). He also corresponded regularly with Bradley, Knight, Leonard, Olsson, and others he had known at Ithaca. In 1928 he returned to Cornell to attend the Fourth International Congress of Entomology; there he agreed to turn over his immature Tipulidae to J. Speed Rogers (University of Florida) and to let him pursue studies on tipulid ecology (Byers, 1982). His last visit to Cornell was in early 1965 when he spent "two wonderful and exciting days" (112) with Professor Bradley and others.

Alexander's accomplishments in teaching, research, and administration during his 37 years at the University of Massachusetts are well known (see Gurney, 1959; Byers, 1982). Students in his classes were "inspired at least a little, in many cases deeply, by his personal magnetism and enthusiasm" (Gurney, 1959). His administrative duties included serving as Head of Entomology from 1930 until his retirement in 1959, Head of the Department of Entomology and Zoology (1938-1948), Acting Dean of the School of Science (1945-1946), and Dean (1946-1952) (Gurney, 1959). And, of course, there was a steady outpouring of taxonomic papers. From 1927 to 1946 he kept an annual record of the number of new species described, with the number of lifetime species and notes to explain "poor" years: illness, the deaths of his father and sister in 1932, large numbers of figures required for particular papers,

and disturbed conditions during World War II (113). He learned in 1928 that according to the staff of *Zoological Record* he had described the largest number of new species in one family (114). And yet he tried to approach his work with a "humble spirit," in contrast to his graduate years at Cornell (and in Kansas and Illinois) when he figured he had "mastered the group" (115). In 1938 he wrote Bradley that new species number 5,000 had been described (116). Less than twenty years later Mort Leonard was astonished to learn that his friend had at least 1,000 more undescribed forms on hand. "If you can only keep on Chuck you may make 10,000 yet, although that is almost too fantastic a figure for me to imagine—or would be if it were anyone else at all but you" (117). Continuing toward that goal, Alexander wrote Bradley in 1965: "Your being able to do the fine work that you are accomplishing on the Scoliidae has encouraged me to believe that I may be privileged to keep up my own work until I drop, as they say" (118). In the early 1970's he attained his goal of describing 10,000 new species in a single family. Well aware of that figure's significance, he had told Leonard shortly before: "As you know, and as we have mentioned various times before, no one ever has described that number of species in a single family, either in plants or animals. Personally, I do not think anyone has described even half that number, and it seems certain it never will be done again, chiefly because of the depletion in numbers of possible new species" (119).

Alexander described his last species in May 1979 (120) and, upon Mabel's death on September 24 of that year, seemed to lose interest in crane flies, even though an estimated 4,000 new species in unopened envelopes and packages awaited description. "It's never ending. I need another lifetime, that's all" (121). But the death of his beloved wife was devastating: "It is a very, very lonely life I lead these days without her" (122). Apparently preparing for the end, he transferred his library and tipulid collection to the National Museum of Natural History in Washington in spring 1981. He died at his home on December 3.

For more than forty years he had expressed an interest in willing money to U.S. entomological societies (123). After his death several societies were notified by probate court that they would receive a sum from the Alexander estate, to be used for publication purposes (Gurney, 1982). Wilkinson (1984) informed dipterists of the availability of Alexander's papers and other materials, which occupy about 60 shelf feet in the Smithsonian Archives.

In a biographical sketch of his longtime friend, George Byers (1982) wrote: "When a man of great accomplishments has lived into his ninety-third year, it seems more fitting to commemorate his long and purposeful life than to mourn his death"—hence the desire for my own tribute to this unforgettable scholar and gentleman.

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#### NOTES

1. J. Chester Bradley to C. P. Alexander, Jan. 23, 1970. Charles P. Alexander Papers, circa 1895–1979, Smithsonian Institution Archives, Washington, D.C., Record Unit 7298; hereafter this collection is abbreviated as Alexander Papers, SIA.
2. Alexander to A. G. Wheeler, Jr., Apr. 8, 1980.
3. Alexander to Ashley B. Gurney, Aug. 28, 1979; "Personal Record of Charles P. Alexander," and "Charles Paul Alexander," Alexander Papers, SIA; "Entomology at Cornell 1909–1917, Recollections of Charles Paul Alexander," Comstock Memorial Library, Cornell University, Ithaca, New York (hereafter Entomology at Cornell, CML). Charles gave his mother's first name variously as *Janet* ("Charles Paul Alexander," Alexander Papers, SIA), *Jane* ("Entomology at Cornell," CML), and *Jennie* (biographical data in Alexander's alumni file, Department of Manuscripts and University Archives, Cornell University, Ithaca, New York) (hereafter Alumni File, CU). His "Personal Record" is an 8-page account (typed from handwritten sheets) covering 1889–1915.



4. Alumni File, CU.
5. "Charles Paul Alexander," Alexander Papers, SIA.
6. Alexander to Gurney, Aug. 28, 1979.
7. "Personal Record," Alexander Papers, SIA.
8. Ibid.
9. Ibid.
10. Alexander to Axel Olsson, Sept. 6, 1972, and Olsson to Alexander, Apr. 30, 1974, Alexander Papers, SIA.
11. "Personal Record," Alexander Papers, SIA.
12. Olsson to Alexander, Apr. 30, 1974, Alexander Papers, SIA.
13. Alexander to Olsson, May 12, 1974, Alexander Papers, SIA.
14. "Personal Record," and notebook on "Birds of Fulton Co.," Alexander Papers, SIA.
15. "Published Writings of Chas. P. Alexander" [1903-1910], Alexander Papers, SIA.
16. "Personal Record," Alexander Papers, SIA.
17. Alexander to Olsson, Mar. 15, 1974, Alexander Papers, SIA.
18. For biographical information on William Prindle Alexander (1881-1956), see A. B. Gurney, "Charles Paul Alexander," *Fernald Club Yearbook* (Fernald Entomol. Club, Univ. Massachusetts), 28 (1959), 1-6, and *Sanctuary News* (Nature Sanc. Soc. West. New York, Buffalo), 16 (1956), 1-4.
19. See *Leader-Republican* (Gloversville, New York), Aug. 28, 1939, p. 8, Alexander Papers, SIA.
20. William's parents sent him to study at the Conservatory of Music in Leipzig during 1900-1905, Alumni File, CU; "Prof. William P. Alexander," *Buffalo Courier-Express*, Oct. 1, 1956, Alexander Papers, SIA.
21. "Charles Paul Alexander," Alexander Papers, SIA.
22. Ibid.
23. Alexander to Minerva Fonda, Nov. 18, 1952, Alexander Papers, SIA.
24. "Charles Paul Alexander," Alexander Papers, SIA.
25. "Personal Record," Alexander Papers, SIA.
26. "Entomology at Cornell," CML.
27. Alexander to H. B. Hungerford, Mar. 31, 1937, Alexander Papers, SIA. Although Alexander's figure was accurate for his time, the number of birds is now thought to be about 9,000; see W. J. Bock and J. Farrand, Jr., "The number of species and genera of recent birds: a contribution to comparative systematics," *Am. Mus. Novitates*, 2703 (1980), 1-29.
28. "Personal Record," Alexander Papers, SIA. Early in his career, Alexander was able to meet (in addition to Needham) at least one other specialist. During Thanksgiving vacation 1910, he and a fellow Cornell student, M. D. Leonard, visited Van Duzee at his home in Buffalo. Alexander characterized the noted hemipterist as "exceedingly enthusiastic, more so than any collector I have ever known." "Diary, July-Nov. 1910," Alexander Papers, SIA.
29. "Entomology at Cornell," CML.
30. "Personal Record," Alexander Papers, SIA.
31. Ibid.
32. Ibid.
33. Ibid.
34. "Entomology at Cornell," CML.
35. Alexander to J. G. Needham, May 2, 1936, Alexander Papers, SIA.
36. Alexander to Olsson, Mar. 15, 1974, Alexander Papers, SIA.
37. "Personal Record," Alexander Papers, SIA. Completion of the language requirement appeased David F. Hoy, Cornell's legendary, tough-but-fair Director of Admissions and Registrar. It is ironic that he initially was denied by Hoy, who himself had botanical interests,

having completed in 1893 an M. S. degree at Cornell on the flora of Delaware Co., New York. A. H. Wright, "Pre-Cornell and early Cornell. David Fletcher Hoy," *Stud. in Hist.*, 30 (n.d., 1964?), 1-6.

38. Ibid.

39. "Data for Insects, Take of 1909," a notebook, Alexander Papers, SIA.

40. "Personal Record," Alexander Papers, SIA.

41. Ibid.

42. Ibid.

43. Alexander soon reduced *Sacandaga* to a subgenus of *Rhabdomastix* Skuse. "Neotropical Tipulidae in the Hungarian National Museum (Diptera—III)," *Entomol. News*, 25 (1914), 211.

44. Alexander to Wheeler, Apr. 8, 1980.

45. Alexander to Olsson, Mar. 15, 1974, Alexander Papers, SIA.

46. "Personal Record," Alexander Papers, SIA.

47. Alexander to Hungerford, Mar. 31, 1937, Alexander Papers, SIA.

48. "Entomology at Cornell," CML.

49. Alexander to Wheeler, n.d., but late 1978.

50. Alexander to Hungerford, Mar. 31, 1937, Alexander Papers, SIA.

51. "Personal Record," Alexander Papers, SIA.

52. "Entomology at Cornell," CML.

53. Alexander to Wheeler, Jan. 7, 1977. In contrast to this formal greeting, Alexander later was known to students by the nickname "Alex." "Write-up, Cornell 1913 Class Book," Alumni File, CU.

54. Alexander to Wheeler, n.d., but late 1978.

55. Alexander to M. D. Leonard, Sept. 24, 1959, Alexander Papers, SIA.

56. "Personal Record," Alexander Papers, SIA.

57. Ibid.

58. "Entomology at Cornell," CML.

59. "Personal Record," Alexander Papers, SIA.

60. Ibid.

61. Alexander to John Stoffolano, July 15, 1976, accepting, in absentia, the L. O. Howard Award, Eastern Branch, Entomological Society of America, presented Aug. 24, 1976, during the XV International Congress of Entomology, Washington, D.C., Alexander Papers, SIA.

62. Alexander to Bradley, Mar. 16, 1938, Alexander Papers, SIA.

63. "Personal Record," Alexander Papers, SIA.

64. "Entomology at Cornell," CML.

65. "Diary, July–November, 1910," Alexander Papers, SIA.

66. "Personal Record," Alexander Papers, SIA.

67. Ibid.

68. Ibid.

69. Ibid.

70. "Entomology at Cornell," CML.

71. Ibid.; Cornell class notebook, Alexander Papers, SIA.

72. Alexander to Olsson, Mar. 15, 1974, Alexander Papers, SIA.

73. In January 1911 Olsson transferred to Cornell from Boston Tech (now Massachusetts Institute of Technology) and took a room at Shipmans next to Alexander; Olsson to Alexander, Apr. 30, 1974, Alexander Papers, SIA. Axel Adolf Olsson (1889–1977) became a well-known geologist and paleontologist and was a founder of the Paleontological Research Institute, Ithaca, New York. Biographical data in Olsson's alumni file, CU.

74. Alexander to Olsson, Sept. 20, 1970; during 1909–1912 Alexander kept a notebook of Fulton Co. plants, "Flora Fultoniensis," which contained about 560 taxa, Alexander Papers, SIA.

75. Alexander to Olsson, Mar. 15, 1974, Alexander Papers, SIA. See also E. H. Smith, "The Comstocks and Cornell: in the people's service," *Annu. Rev. Entomol.*, 21 (1976), 15.
76. Alexander to Wheeler, Apr. 8, 1980.
77. Alexander to Leonard and his wife Doris, Feb. 26, 1974, Alexander Papers, SIA.
78. "Personal Record," Alexander Papers, SIA.
79. Alexander to Olsson, Mar. 15, 1974, Alexander Papers, SIA.
80. Alexander to Hungerford, Mar. 31, 1937, Alexander Papers, SIA.
81. "Personal Record," Alexander Papers, SIA.
82. Ibid.
83. Alexander to Olsson, Mar. 15, 1974, Alexander Papers, SIA.
84. Alexander to Wheeler, Apr. 8, 1980. During the academic year 1909–1910, Alexander had served in Company A, infantry, as a cadet in the university army corps, Alumni File, CU. See figure 6.
85. Alexander to Wheeler, Jan. 7, 1977.
86. "Entomology at Cornell," CML.
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89. *The Cornellian*, 45 (1913), 329.
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94. Alexander to H. H. Knight, May 25 and Nov. 23, 1975, Alexander Papers, SIA; Alexander to Wheeler, June 18, 1978, and Apr. 8, 1980.
95. *The Cornellian*, 45 (1913), 329.
96. O. A. Johannsen to Alexander, n.d., but circa 1919, Alexander Papers, SIA.
97. Alexander to Leonard and wife Doris, Nov. 17, 1964, Alexander Papers, SIA.
98. Alexander to Bradley, Nov. 1, 1920, Alexander Papers, SIA.
99. Alexander to Bradley, Nov. 22, 1920, Alexander Papers, SIA.
100. Alexander to Olsson, Sept. 20, 1970, Alexander Papers, SIA.
101. Alexander to Olsson, Mar. 15, 1974, Alexander Papers, SIA.
102. "Personal Record," Alexander Papers, SIA.
103. Ibid.; Alexander to Olsson, Sept. 6, 1972, Alexander Papers, SIA.
104. Alexander to Olsson, Sept. 20, 1970, and Mar. 15, 1974, Alexander Papers, SIA.
105. John Sherwood, "'Doc Alex': The World's Greatest Crane Fly Electronic Data Bank," *The Washington Star*, Nov. 22, 1979, Sec. D, pp. 1, 7.
106. Alexander to Olsson, Mar. 15, 1974, and G. W. Byers, Oct. 5, 1975, Alexander Papers, SIA; Alexander to Wheeler, Apr. 8, 1980.
107. Alexander to Wheeler, Apr. 8, 1980.
108. Alexander to Hungerford, Feb. 29, 1924, Alexander Papers, SIA.
109. Alexander to Leonard and wife Doris, Nov. 17, 1964, Alexander Papers, SIA.
110. Alexander to Wheeler, Apr. 8, 1980.
111. Sherwood, 'Doc Alex.'
112. Alexander to Bradley, Apr. 21, 1965, Alexander Papers, SIA.
113. "Record of New Species," Alexander Papers, SIA.
114. Alexander to Hungerford, Mar. 31, 1937, Alexander Papers, SIA.
115. Ibid.
116. Alexander to Bradley, Mar. 16, 1938, Alexander Papers, SIA.
117. Leonard to Alexander, Oct. 27, 1957, Alexander Papers, SIA.
118. Alexander to Bradley, Apr. 21, 1965, Alexander Papers, SIA.
119. Alexander to Leonard and wife Doris, Mar. 8, 1970, Alexander Papers, SIA.

120. Sherwood, 'Doc Alex.'

121. Ibid.

122. Ibid.

123. Alexander to Hungerford, Mar. 31, 1937, Alexander Papers, SIA.

## A REVISION OF THE PENTATOMINE GENUS *SERDIA* STÅL, 1860 (PENTATOMIDAE: HEMIPTERA)

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**Abstract.**—The stink bug genus *Serdia* is divisible into two subgenera: *Brasiliicola* Kirkaldy and *Serdia* Stål. Keys for the separation of each and their included species are provided. To the 7 previously known species of *Serdia* we add 6 new species, all placed in the nominate subgenus: *lobata* from Brazil, *ruckesi* from Peru, *quadridens* from Peru, *delphis* from Ecuador, *beckeri* from Panama and Costa Rica, and *bihamulata* from Venezuela.

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Becker (1967) revised the genus *Serdia* Stål, 1860, redescribing the four species first described by Stål (1860), augmenting the original description of *concolor* Ruckes, 1958, adding *rotundicornis* Becker, 1967, and providing keys to the two subgenera proposed by Kirkaldy (1909) and to the species. Rolston et al. (1980) included *Serdia* in a key to the genera of Western Hemisphere pentatomines characterized by having an abdominal tubercle apposed apically by the ventrally produced metasternum. However, in this key the genus *Elsiella* Froeschner, 1981, also keys with *Serdia*. The 2 genera are separable by the couplet provided by Froeschner (1981) except that antennal segment II of *Serdia* ranges from about  $\frac{1}{5}$  to about  $\frac{3}{5}$  as long as segment III. Here we add six new species to the nominate subgenus of *Serdia*, modify Becker's keys to the subgenera and species of the subgenus *Brasiliicola*, and give a key to the species of the nominate subgenus.

All measurements in the descriptions of new species are from the holotype unless explicitly stated otherwise. Length of the body was measured from the apex of the juga to the apex of the hemelytral membrane. Width was measured across the pronotal humeri. Length of the head was measured from the apex of the juga to an imaginary line joining the ocelli. Width of the head was the greatest anteocular width.

### KEYS TO SUBGENERA AND SPECIES OF *Serdia*

#### Key to the Subgenera of *Serdia* Stål, 1860 (modified from Becker, 1967)

1. Discal area of abdomen bordered laterally by a row of calloused macules, two to a segment with one anterior to other; black fovea in each basal angle of scutellum bordered mesially by calloused yellowish spot; lateral margins of head parallel, apex broadly rounded ..... subgenus *Brasiliicola* Kirkaldy
- Abdomen and scutellum without calloused macules and spots; lateral margins of head converging toward apex ..... subgenus *Serdia* Stål



Key to the Species of the Subgenus *Brasillicola* Kirkaldy  
(modified from Becker, 1967)

- 1. Size large, male about 14 mm long; body ovate ..... *calligera* Stål
- Size small, male about 11 mm long; body semi-rhomboidal, abdomen truncated at apex ..... *costalis* Ruckes

Key to the Species of the Subgenus *Serdia* Stål

- 1. Humeral angles expanded, lobate, produced laterad of hemelytra at base by more than width of eye ..... 2
- Humeral angles produced laterad of hemelytra at base by less than width of eye .. 4
- 2(1). Connexiva alternated ..... *apicicornis* Stål
- Connexiva unicolorous ..... 3
- 3(2). Humeral lobes directed laterad ..... *rotundicornis* Becker
- Humeral lobes directed anterolaterad ..... *lobata*, new species
- 4(1). Pale wedge along costal margin of each hemelytron includes most of exocorium basally, gradually narrows distally ..... *limbatipennis* Stål
- Exocoria concolorous with hemelytral discs or only narrow costal margins pale basally ..... 5
- 5(4). Apex of scutellum conspicuously pale to unaided eye ..... *ruckesi*, new species
- Scutellum nearly uniform in color to unaided eye ..... 6
- 6(5). Ventral margin of mesosternal carina linear in profile; red line present on lateral submargins of pronotum and connexiva ..... *inspersipes* Stål
- Ventral margin of mesosternal carina uneven in profile; lateral submargins of pronotum and connexiva without red line ..... 7
- 7(6). Abdominal venter with broad, diffuse, fuscous vitta mesially, sometimes expanded to cover most of venter and juga nearly or just contiguous apically ..... *quadridens*, new species
- Abdominal venter yellowish brown with fuscous limited to suffusion around punctures, or if vittate juga well separated apically ..... 8
- 8(7). Apex of abdominal tubercle broadly rounded (Fig. 8) ..... 9
- Apex of abdominal tubercle narrowly rounded to acute (Fig. 9) ..... 10
- 9(8). Rostrum not quite attaining metasternum; costal margin of hemelytra narrowly pale toward base; antennal segment V white; anterolateral margins of pronotum carinate ..... *concolor* Ruckes
- Rostrum attaining metasternum; costal margin of hemelytra and last antennal segment brown; anterolateral margins of pronotum not carinate ..... *delphis*, new species
- 10(8). Mesosternum nearly impunctate on both sides of carina; length about 14 mm; pygophore lacking hamuli (Fig. 2)..... *beckeri*, new species
- Mesosternum with moderately dense punctation on both sides of carina; length of male about 9.5 mm; pygophore with erect hamulus just mesad of each posterolateral angle (Fig. 3) ..... *bihamulata*, new species

***Serdia lobata*, new species**

*Description.* Elongate, with humeri produced dorsad and anterolaterad as lobes. Sordid brown, irregularly punctate dorsally. Length 13.5 mm, width 7.3 mm.

Head: Length 1.8 mm, width 1.75 mm. Juga strongly surpassing tylus but not contiguous, leaving narrow cleft between their apices. Juga darkly punctate, this

punctuation extending posteriorly onto base of head as pair of vittae, one on each side just mesad of each ocellus. Antennal segment I fuscous, segments II–IV dark brown (V missing). Segmental lengths 0.8, 0.4, 2.0, 1.7,—mm. Rostrum attaining middle of metasternum.

Thorax: Anterolateral margins somewhat explanate, largely impunctate, without setae, concave from dorsal view, yellow as are posterolateral margins; humeri fuscous from crowded dark punctuation. Scutellum with dark fovea in each basal angle and at apex a dark patch on each side of elongate pale macule. Profile of mesosternal carina even along ventral margin. Metasternum weakly emarginate for reception of abdominal tubercle. Exocoria distinctly paler than hemelytral disc, delineated mesially by row of deep, dark punctures. Membrane vitreous, veins contrastingly dark. Legs with small, scattered maculae.

Abdomen: Tubercle flat, triangular from ventral view, apex narrowly rounded. Spiracles ringed with black. Posterolateral angles of sternites with black spicule. Connexiva light brown with dense concolorous punctations.

Genitalia: Posteroventral emargination of pygophore encompassing mesial, lingulate protuberance from inferior ridge (Fig. 5); protuberance dark, strigose, its posterior margin trisinate from ventral view. Parameres robust, thick, blade-like, obtuse apically. Female unknown.

Holotype: ♂; labeled (a) "BRAZIL, Sao Paulo: Serra Bocaina, S.J. Barreiro 1650 m." (b) "OCT.–NOV. 1969 Alvarenga & Seabra." Deposited in the American Museum of Natural History.

Comments: Allied to *apicicornis* but differing especially in having the connexiva immaculate, much smaller macules on the legs, the metasternum weakly emarginate posteriorly, and much longer parameres, which in *apicicornis* can be seen only by removing the proctiger.

### *Serdia ruckesi*, new species

*Description.* Elongate-ovate; shiny olivaceous brown dorsally; mesial line on base of head and anterior disc of pronotum, irregular transverse fascia between humeri, and apex of scutellum, yellow-ivory; obscure fuscous macule on disc of each corium with ivory spot at anterior margin. Distal  $\frac{7}{10}$  of antennal segment IV and about  $\frac{1}{2}$  of segment V beginning  $\frac{1}{5}$  its length from base, fuscous. Length 15.5 mm, width 8.0 mm.

Head: Length 2.1 mm, width 2.0 mm. Jugal converging before tylus, nearly contiguous. Rostrum just attaining metasternum. Antennal segments 0.9, 0.8, 2.1, 2.5, 3.2 mm long.

Thorax: Humeri obtusely angular, slightly produced; anterolateral margins of pronotum neither carinate nor reflexed, distinctly concave from dorsal view, sparsely fringed with long setae. Fovea in each basal angle of scutellum black; apex impunctate. Mesosternum feebly produced in middle, ventral margin in profile nearly straight but projecting a little farther ventrad at procoxae. Metasternum broadly and deeply emarginate for reception of abdominal tubercle. Legs maculate.

Abdomen: Posterolateral angles of sternites with spicule. Spiracles ringed with black. Basal tubercle strongly developed, broad, flat, obtuse at apex.

Genitalia: Posterior border of pygophore broadly concave, notched at lateral angles,

each angle attended mesad by thick tuft of setae; posteroventral face with lunate excavation subtending posterior border mesially (Fig. 7). Parameres elongate, thick, narrowing from flattened basal half to terete, sinuate apical half. Females unknown.

Holotype: ♂; labeled "Peru, Dpto. La Libertad, Cumpang above Uctubamba. 2625 M. 16 X 1979, L. J. Barkley." Deposited in the American Museum of Natural History.

Paratypes: 2♂♂; 1 labeled same as holotype; 1 labeled "Peru, Dpto. Cajamarca, Batan to Machete on Zapalache-Carmen trail, 2250–2050 m. 14-June–9 July 1980." Deposited in collections of the authors.

Comments: This species is distinguished by the structure of the pygophore and by the yellow-ivory markings on the dorsum.

### ***Serdia quadridens*, new species**

*Description.* Elongate oval; dark sordid brown, densely punctate. Length 13–15 mm, width 6.6–7.5 mm.

Head: Length 1.95 mm, width 1.9 mm. Juga convergent, nearly or just contiguous before tylus. Rostrum attaining middle of metasternum. Antennal segments 0.8, 0.6, 2.0, 2.2, 2.9 mm long.

Thorax: Carina along very slightly concave anterolateral margins of pronotum becoming obsolete anteriorly, bearing sparse fringe of moderately long setae; humeral angles narrowly rounded, slightly produced. Small, pustular macule on each corium at end of R+M vein usually pale; membrane infuscated. Mesosternal carina nearly flat except anteriorly, feebly produced in middle, gradually more so anteriorly to form stout, compressed, pale projection between procoxae. Metasternum scatteringly punctate, broadly and deeply notched for reception of abdominal tubercle. Legs maculate.

Abdomen: Stout basal tubercle flat ventrally, narrowly rounded apically. Spiracles ringed with black. Broad, diffuse, mesial vitta on venter fuscous, sometimes expanded to cover most of venter. Connexival color and punctation like adjacent area of venter, brown with dark, moderately dense punctation.

Genitalia: Posterior margin of pygophore broadly V-shaped, heavily setose, notched mesially; notch attended by 4 black, tuberculate teeth. Parameres with basal flange and elongate apical shaft; shaft terete, thin; bent slightly mesoventrad apically. Female unknown.

Holotype: ♂; labeled "Peru, Dpto. La Libertad Cumpang. above Uctubamba. 2625 M. 13 X 1979. L. J. Barkley." Deposited in the American Museum of Natural History.

Paratypes: 3♂♂; labeled same as holotype. Deposited in the United States National Museum and collections of the authors.

Comments: This species can be distinguished by the incomplete carina on the anterolateral margin of the pronotum, the fuscous mesial vitta on the abdominal venter, and the 4 black tubercles on the posterior pygophoral border.

### ***Serdia delphis*, new species**

*Description.* Elongate-ovoid; sordid yellowish-brown. Fovea in each basal angle of scutellum darkened. Length 14.0 mm, width 6.6 mm.

Head: Length 1.9 mm, width 1.8 mm. Testaceous punctures numerous on juga, tylus and disc of head; juga prolonged beyond tylus but not contiguous, leaving

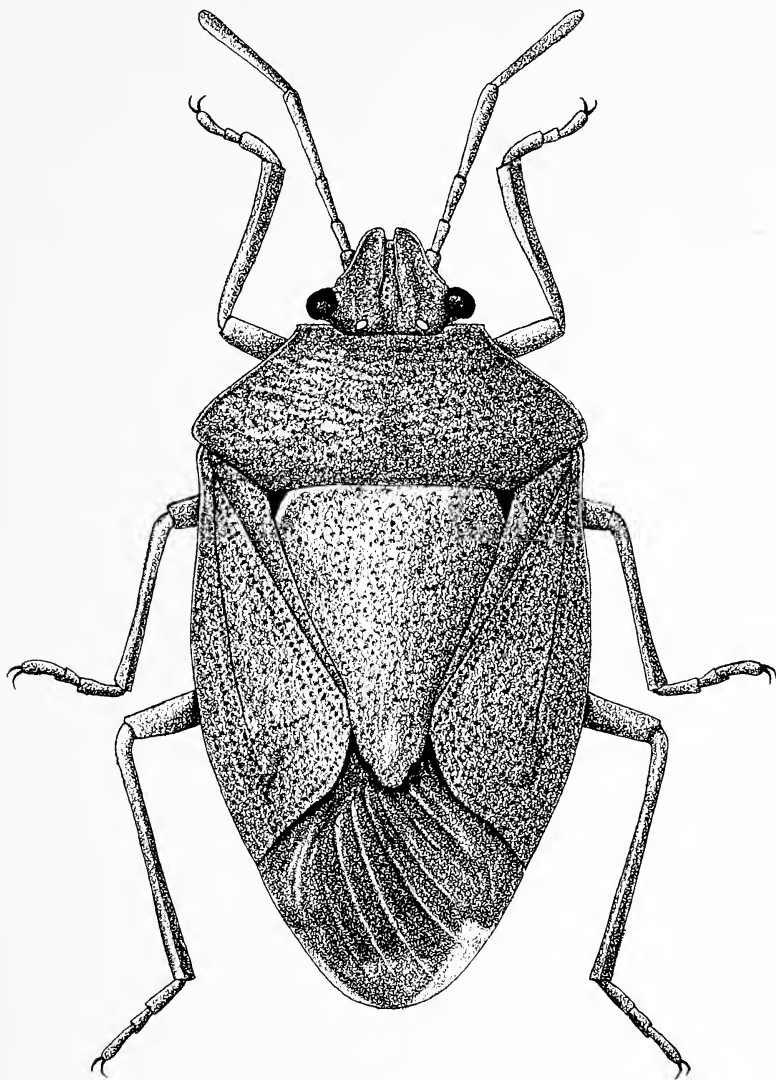
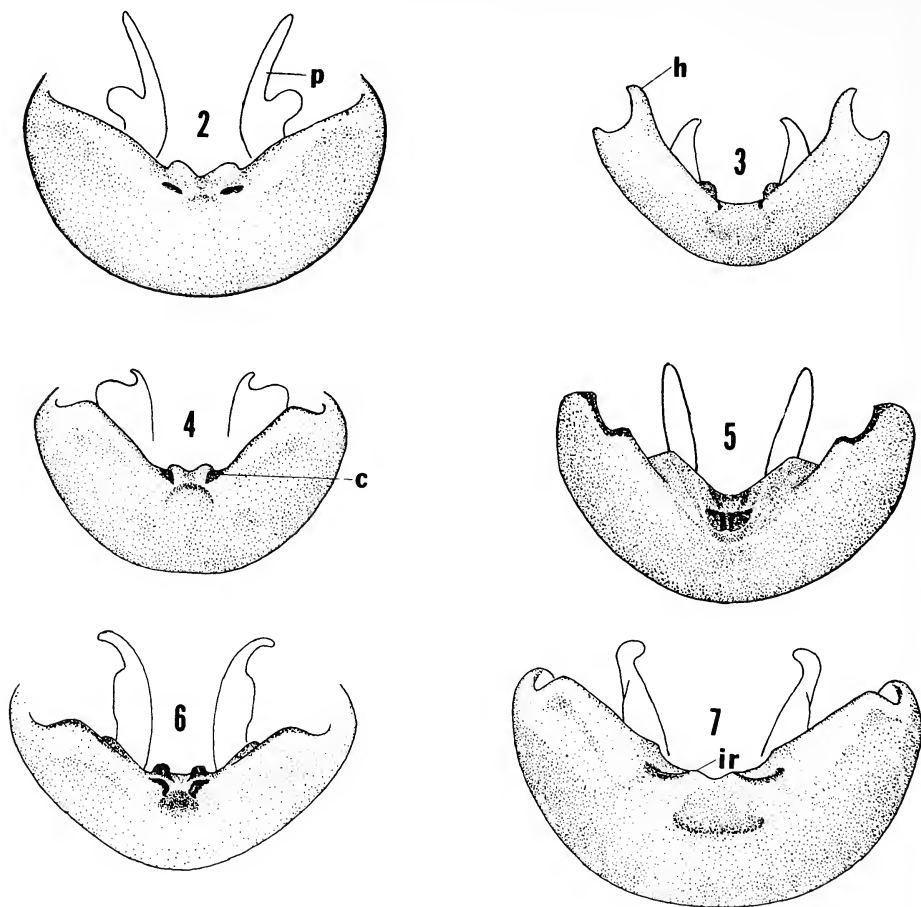


Fig. 1. *Serdia beckeri*.

elongate cleft between apices. Rostrum surpassing anterior margin of metasternum but not attaining middle. Antennae tan, 2 basal segments testaceously dotted; segmental lengths (from paratype) 0.9, 0.6, 1.6, 1.8, 2.4 mm.

Thorax: Dorsal pronotal punctation denser and darker near margins; anterolateral margins not clearly carinate, weakly concave from dorsal view, bearing sparse fringe of long setae; humeri subangular, slightly produced. Scutellum evenly punctate on disc; punctation obscure apically; apex subacuminate. Membrane of hemelytra lightly fumose, veins darker. Mesosternum weakly produced at middle, increasingly more



Figs. 2-7. Pygophore, caudal view with proctiger omitted. 2. *beckeri*, paramere (p). 3. *bihamulata*, hamulus (h). 4. *delphis*, cusp (c). 5. *lobata*. 6. *quadridens*. 7. *ruckesi*, inferior ridge (ir).

so toward procoxae, terminating in wedge between procoxae. Metasternum broadly emarginate for reception of abdominal tubercle. Legs with scattered brown maculae.

Abdomen: Basal tubercle broadly rounded apically, flat, reaching posterior margin of metacoxae. Spiracles obscurely ringed with brown to nearly concolorous with sternites. Black spicule present on posterolateral angles of sternites. Connexiva yellowish brown with sparse, obscure punctation.

Genitalia: Lateral margins of pygophore bearing entally directed dark tooth on each side. Posteroventral border emarginate mesially, forming cavity enclosed entally by inferior ridge; emargination tended on each side by dark cusp (Fig. 4). Lateral process of parameres lobate; apical process elongate, sinuate, terminally acuminate.

First gonocoxae somewhat tumescent, contiguous mesially, concealing triangulum. Eighth paratergites spinose apically.





Figs. 8, 9. Abdominal tubercle in apposition to metasternum. 8. *S. delphis*. 9. *S. beckeri*.

Holotype: ♂; labeled (a) "Mt. Tungurahua, III:4:37, Ecuad." (b) "Col. by Wm. Clarke-MacIntyre" (c) "'Chaupi' 3000 m." (d) "Chicago N.H. Mus. Collection (ex W. J. Gerhard Colln.)." Deposited in the American Museum of Natural History.

Paratype: ♀; labeled same as holotype. Deposited in L. H. Rolston collection.

Comments: The male genitalia are similar to those of *beckeri*, but this species differs from *beckeri* in that the anterolateral pronotal margins do not have a reflexed carina, the mesosternal carina is less produced at the procoxae, and the abdominal tubercle is shorter and broadly rounded apically.

#### *Serdia beckeri*, new species

*Description.* Elongate-ovate; sordid tan. Fovea in each basal angle of scutellum and small callus on each subapical margin black (Fig. 1). Length 14.2 mm, width 6.9 mm.

Head: Length 2.1 mm, width 1.9 mm. Juga longer than tylus but not contiguous, leaving apical cleft. Rostrum attaining middle of metasternum. Antennal segments I–IV sordid tan, thickly dotted with fuscous (V missing); segmented lengths 0.8, 0.9, 1.8, 2.1, —.

Thorax: Anterolateral pronotal margins carinate, slightly reflexed, sparsely fringed with long setae; humeri rounded, not produced. Mesosternum weakly produced at middle, strongly so anteriorly, carina barely reaching between procoxae. Metasternum deeply emarginate for reception of abdominal tubercle. Legs rufescent, obscurely maculate.

Abdomen: Mesial tubercle elongate, reaching middle of metacoxae, subacuminate, flat ventrally. Spiracles black. Posterolateral angles of sternites acute but lacking spicule. Connexival color and punctation conforming to adjacent area of venter, sordid tan with dark punctation. Venter with or without mesial vitta.

Genitalia: Mesial depression in posterior pygophoral border supertended by obtusely bidentate inferior ridge and flanked on each side by darkened but otherwise inconspicuous cusp (Fig. 2). Parameres toward base expanded laterad into obtuse process; apical process narrowly terete, elongate. Female unknown.

Holotype: ♂; labeled "PANAMA, Chiriqui Dist. Renacimiento Santa Clara, 4000' V-23-26 1977." Deposited in the American Museum Natural History.

Paratype: ♂; labeled "C.R., Punt. Monteverde Cloud For. Res. V-27, 31-84. Riley, Rider & LeDoux." Deposited in collection of junior author.

Comments: Related to *delphis* by the similarity of male genitalia but differing primarily in having reflexed, carinate pronotal margins, the mesosternal carina more prominently produced at the procoxae, and a subacuminate abdominal tubercle.

### ***Serdia bihamulata*, new species**

*Description.* Obovate; dull tan dorsally, shining sordid ventrally. Fovea in each basal angle of scutellum and subapical scutellar margin black. Length 9.7 mm, width 5.5 mm.

Head: Length 1.6 mm, width 1.5 mm. Juga broadly contiguous before tylus. Rostrum not quite attaining middle of metasternum. Antennal segments III, IV black, V yellow; segmental lengths 0.6, 0.7, 1.1, 1.6, 1.6 mm.

Thorax: Anterolateral margins with reflexed carina, slightly concave from dorsal view, with sparse fringe of short setae; humeri somewhat produced, moderately rounded. Mesosternum moderately produced at middle, rapidly becoming more so at procoxae. Metasternum conspicuously emarginate for reception of abdominal tubercle. Legs maculate.

Abdomen: Tubercle subspinose apically. Posterolateral angles of sternites without spicules, those of segments 6 and 7 slightly produced. Spiracles ringed with black. Connexiva dull tan with dense, dark punctation.

Genitalia: Hamulus just mesad of posterolateral pygophoral angles erect, bent laterad apically; posterior pygophoral border mesially emarginate, subtended by semi-oval depression with small dark cusp on each side (Fig. 3). Parameres tapering to blunt apex, with small lateral tubercle where bent at middle. Female unknown.

Holotype: ♂; labeled "VENEZUELA, Aragua, Rancho Grande, 1500–1900 m., May 8, 1978. O'Brien & Marshall." Deposited in the American Museum of Natural History.

Comments: Distinguished by its small size and erect hamuli on the pygophore.

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## NAMES PROPOSED AND TAXONOMIC PUBLICATIONS BY HERBERT RUCKES (1895-1965)

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*Abstract.*—A list of names proposed and a bibliography are presented for Herbert Ruckes.

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Although Dr. Herbert Ruckes did most of his taxonomic work at the American Museum of Natural History after retiring from The City College of the City University of New York (Anon., 1966), he was nonetheless a productive taxonomist. He had several projects in progress at the time of his death and left in various museums specimens that are labeled as type material. These specimens are troublesome to curators and researchers because the names proposed by Dr. Ruckes and validated by publication have not been compiled previously. As a service to those concerned, the taxonomic publications and available names proposed by Dr. Ruckes are listed here.

### LIST OF NAMES PROPOSED AND THEIR CURRENT STATUS IF CHANGED

#### COREOIDEA

##### COREIDAE

*Chariesterus bahamensis*. 1955b:6-7, figs. 2, 14, 19.

*C. pardalinus*. 1955b:12-13, figs. 7, 20.

*Mozena arizonensis*. 1955a:2-4.

*M. lunata rufescens*. 1955a:7-8.

*M. pallisteri*. 1955a:5-7.

*M. tomentosa*. 1955a:4-5.

#### PENTATOMOIDEA

##### ACANTHOSOMATIDAE

*Elasmotherus gracilis*. 1963:356, fig. 10b.

##### CYDNIDAE

*Aethus diminutus*. 1952b:2-4.

##### PENTATOMIDAE

##### Asopinae

*Bulbostethus*. 1960b:287-288.

*B. transversalis*. 1963:329-331, fig. 5a, b.

**Ponapea.** 1963:325–326.

*P. arachnoides.* 1963:326–328, fig. 4.

## Discocephalinae

### Discocephalini

**Acclivilamna.** 1966c:39–40.

*Alcippus dimidiatus.* 1959f:97–100, fig. 1a, b, c.

**Allinocoris.** 1966c:29.

**Alveostethus.** 1966c:31–33.

*Antiteuchus (A.) bartletti.* 1964a:97–98, figs. 72–74.

*A. (A.) confinium.* 1964a:94–95, figs. 63–65.

*A. (A.) costaricensis.* 1964a:80–81, figs. 40, 41.

*A. (A.) cuspidatus.* 1964a:98–100, figs. 69–71.

*A. (A.) fulvescens.* 1964a:73–74, figs. 29–31.

*A. (A.) guianensis.* 1964a:95–96, figs. 66–68.

*A. (A.) maculosus.* 1964a:81, 83, figs. 45, 46.

*A. (A.) mimeticus.* 1964a:100–101, figs. 75–77.

*A. (A.) nebulosus.* 1964a:89–91, figs. 10, 53–55.

*A. (A.) nigricans.* 1964a:71–72, figs. 25, 26.

*A. (A.) peruensis.* 1964a:85–86, figs. 3, 47–49.

*A. (A.) pictus.* 1964a:79–80, fig. 39.

*A. (A.) punctissimus.* 1964a:92–94, figs. 60–62.

*A. (A.) radians.* 1964a:65–66, 71, figs. 15, 16.

*A. (A.) subimpunctatus.* 1964a:64–65.

*A. (A.) tripterus limbativentris.* 1964a:77–78.

*A. (A.) varians.* 1964a:91–92, figs. 56–59.

**Callostethus.** 1961b:153–156.

**Dentocephala.** 1960a:1–3. = *Harpogaster* (Pirán, 1962:8).

*Dentocephala parva.* 1960a:3, 5, figs. 1, 2. = *Harpogaster willineri* (Pirán, 1962:8).

*Dinocoris binotata.* 1958b:6–7. = *D. corrosus* (Pirán, 1962:6).

*D. robustus.* 1959b:147–148.

*D. rufitarsus.* 1958b:4–5.

*Dryptocephala crenata.* 1966d:13–14, fig. 3.

*D. lipoloba.* 1966d:18–20, figs. 7, 13, 14, 25, 26.

*D. maculosa.* 1966d:17–18, figs. 6, 15, 16, 23, 24.

*D. nigricornis.* 1966d:14–16, fig. 4.

*Eurystethus (E.) ellipsoidalis.* 1958b:1–4, fig. 1.

*E. (E.) macroconus.* 1966b:8–10, fig. 4.

*E. (E.) ornatus.* 1966b:10–12, fig. 11.

*E. (E.) ovalis.* 1966b:17–18, fig. 14.

*E. (E.) pallescens.* 1966b:18–20, fig. 15.

*E. (E.) parvulus.* 1966b:13–15, fig. 12.

*E. (E.) sordidus.* 1966b:20–22.

*E. (E.) spurculus.* 1966b:15–16, fig. 13.

*E.* subgen. *Hispidisoma.* 1966b:22–23.

*E. (H.) fulvescens.* 1966b:33–34, figs. 9, 20.

- E. (H.) microlobatus*. 1966b:34–36, figs. 10, 21.  
*E. (H.) nigricornis*. 1966b:25–26, fig. 16.  
*E. (H.) nigroviridis*. 1966b:26–28, figs. 6, 17.  
*E. (H.) punctissimus*. 1966b:24–25.  
*E. (H.) sacculatus*. 1966b:29–30, figs. 3, 8, 18.  
*E. (H.) variegatus*. 1966b:30–32, figs. 2, 7, 19.
- Grassator**. 1965:123, 125.  
*G. reticulatus*. 1965:127–129, figs. 19, 20.  
*G. sinuatus*. 1965:126–127, figs. 17, 18.
- Lineostethus**. 1966c:22–24.
- Mecistorhinus** (*Antiteuchus*) **fuscus**. 1959a:6–8. = *Antiteuchus (A.) fuscus* (Ruckes, 1964a:67).  
*M. coralium*. 1960a:9–10.  
*M. lineatus*. 1959a:2–4.  
*M. panamensis*. 1959a:4–6. = *Antiteuchus (A.) panamensis* (Ruckes, 1961b:152).  
*M. tibialis*. 1959e:2–3.  
*M. variegatus*. 1966a:223–224.
- Neodine tatei**. 1958a:7–8. = *Antiteuchus (Neodine) tatei* (Ruckes, 1961b:153).
- Pandonotum**. 1965:118–119.  
*P. punctiventris*. 1965:119–120, fig. 3.
- Parantiteuchus**. 1962b:95–97.  
*P. hemitholus*. 1962b:97–99, figs. 1, 2.
- Parvamima**. 1960a:6.  
*P. bicolor*. 1960a:7–9, fig. 3.
- Patronatus**. 1965:129–130.  
*P. binotatus*. 1965:130–132, figs. 21–24.  
*P. flavicrus*. 1965:133–134, figs. 28–30.  
*P. punctissimus*. 1965:132–133, figs. 25–27.
- Pelidnocoris haglundii**. 1966e:4–6, figs. 5–8.  
*P. majusculus*. 1966e:6–8, figs. 9, 10.
- Placidocoris**. 1965:114–116.  
*P. bivittatus*. 1965:116, fig. 1.
- Platycarenum** (*Discocephalessa*) **kormilevi**. 1958a:4–7. = *Acclivilamna vicina* (Ruckes, 1966c:40).  
*P. (D.) nigroventris*. 1958a:2–4. = *Grassator nigroventris* (Ruckes, 1965:125).  
*P. (D.) pseudopolitus*. 1957a:17–19. = *Alveostethus pseudopolitus* (Ruckes, 1966c:36).  
*P. (D.) tenebricornis*. 1957a:16–17. = *Lineostethus tenebricornis* (Ruckes, 1966c:24).
- Platycarenum uncinatus**. 1960a:10–12.
- Selenochilus**. 1964b:129–131.  
*S. nitidus*. 1964b:131–132.
- Tetragonotum**. 1965:117.  
*T. megacephalum*. 1965:117–118, fig. 2.
- Uncinala**. 1965:120–121.  
*U. tau*. 1965:121–123, figs. 4–9.
- Unicrus**. 1966c:26–27.



## Ochlerini

**Brachelytron.** 1958a:17-19.

*B. angelicus.* 1958a:19-20, fig. 3.

**Eritrachys.** 1959e:10-11.

*E. bituberculata.* 1959e:11-13, fig. 4.

**Minilincus.** 1958a:14-15. = *Lincus* (Rolston, 1983a:2).

*M. parvulus.* 1958a:15-17, fig. 2. = *Lincus parvulus* (Rolston, 1983a:17).

**Miopygium grossa.** 1958a:8-10.

**Neoadoxoplatys longirostra.** 1959b:149-150.

**Orbatina.** 1961a:228-229.

*O. fuliginia.* 1961a:229-231.

**Schraderia.** 1959e:3-5.

*S. cinctus.* 1959e:8-10, fig. 3.

*S. hughesae.* 1959e:5-8, figs. 1, 2.

**Vauriana.** 1958a:10-12. = *Paralincus* (Rolston, 1983b:183).

*V. bimaculata.* 1958a:12-14, fig. 1. = *P. bimaculatus* (Rolston, 1983b:187).

## Pentatominae

## Halyini

**Brochymena barberi.** 1939b:111-113, fig. 1.

*B. barberi* var. *diluta.* 1939b:113-114.

*B. dilata.* 1939a:239-242, fig.

*B. chelonoides.* 1957a:22-24.

*B. enigmatica.* 1961a:225-227.

*B. exardentia.* 1961a:227-228.

*B. florida.* 1939c:236-238, fig.

*B. humeralis.* 1939b:116-118, fig. 3.

*B. laevigata.* 1957a:19-21.

*B. lineata.* 1939a:236-239, fig.

*B. parva.* 1946a:42-44 (n. name).

*B. splendida.* 1957a:21-22.

*B. usingeri.* 1939b:114-116, fig. 2.

## Mecideini

**Mecidea minor.** 1946b:87-88, figs. D-F.

## Pentatomini

**Banasa grisea.** 1957c:46-47.

**Catacanthus fuchsinus.** 1963:338-339, fig. 6b.

**Disderia inornata.** 1959c:28, 30, figs. 3-5.

**Glaucias eburnopictus.** 1963:347-348, fig. 8b.

*G. fulvescens.* 1963:344-346, fig. 8a.

*G. lucidus.* 1963:342-343, fig. 7a.

- G. lyratum*. 1963:346–347.  
*G. ponapensis*. 1963:348–350, fig. 9.  
*G. robustus*. 1963:343–344, fig. 7b.  
*G. spectabilis*. 1959g:101–103.  
**Marghita**. 1964c:261–262.  
*M. crepuscula*. 1964c:262–265, figs. 1–3.  
*Neottiglossa corona-ciliata*. 1957c:41–42.  
*Odmalea olivacea*. 1959d:55–57. = *Thoreyella brasiliensis* (Rolston, 1978:22).  
*O. quadripunctula modesta*. 1959e:17–18. = *Odmalea concolor* (Rolston, 1978a:23).  
*Oenopiella testacea*. 1959b:150–152. = *Mormidea geographica* (Rolston, 1978b:177).  
**Paratibilis**. 1960a:24–25.  
*P. confusa*. 1960a:25–26.  
**Parvacrena**. 1963:335–336.  
*P. punctata*. 1963:336–337, fig. 6a.  
*Peribalus fulvipes*. 1957c:39–41. = *Holcostethus fulvipes* (McDonald, 1975:252).  
*Plautia cyanoviridis*. 1963:353–355, fig. 10a.  
**Pseudevoplitis**. 1958b:8–9.  
*P. longicornis*. 1959e:13–17, figs. 5, 6.  
*P. paradoxus*. 1958b:9–12, figs. 3, 4.  
**Rio insularis**. 1960a:15–18, figs. 5, 8.  
*R. obscuratus*. 1960a:20–21, fig. 6.  
*R. testaceus*. 1960a:18–20, fig. 9.  
*R. variegatus*. 1960a:21–23, fig. 7.  
**Serdia concolor**. 1958b:12–13.  
*S. costalis*. 1958b:13–15.  
**Thyanta acuminata**. 1956:63–65, fig. 5.  
*T. acuta*. 1952a:67–68.  
*T. bimini*. 1952a:65–67. = *Cyptocephala bimini* (Rolston and McDonald, 1984:77).  
*T. cornuta*. 1956:66–68.  
*T. crinita*. 1957c:44–46.  
*T. humeralis*. 1956:57–59, fig. 2.  
*T. nitidula*. 1956:62–63, fig. 4.  
*T. pallido-virens setosa*. 1957b:17–18.  
*T. pallido-virens spinosa*. 1957b:18–19.  
*T. picturata*. 1957c:42–44. = *Cyptocephala antiguensis* (Rolston, 1972:281; Rolston and McDonald, 1984:77).  
*T. planifrons*. 1956:59–61, fig. 3.  
*T. serratulata*. 1957d:178–179, figs. 5, 6.  
*T. setigera*. 1957d:179–180, figs. 7, 8.  
*T. signoreti*. 1956:65–66, fig. 7.  
*T. spectabilis*. 1957d:175–176, 178, figs. 3, 4.  
*Trichopepla klotsi*. 1937b:2. = *Trichopepla dubia* (McDonald, 1976:15).  
**Zimmeria**. 1958a:20–23. = *Janeirona* (Rolston and McDonald, 1979:200).  
**Zimmerana**. 1962c:234 (n. name). = *Janeirona* (Rolston and McDonald, 1979:200).

## Sciocorini

*Sciocoris crassus*. 1959b:145-147.

## Podopinae

*Scotinophara minor*. 1963:319-320, fig. 3.

## PLATASPIDAE

*Brachyplatys insularis*. 1963:314-316, figs. 1a, 2.

## TAXONOMIC PUBLICATIONS OF HERBERT RUCKES

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- Ruckes, H. 1957c. New species of Pentatomidae from North and South America (Heteroptera) II. Bull. Brooklyn Ent. Soc. 52(2):39–47.
- Ruckes, H. 1957d. Three new species of *Thyanta* Stål (Heteroptera: Pentatomidae). Pan-Pacific Ent. 33(4):175–180.
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- Ruckes, H. 1958b. Some new genera and species of tropical pentatomids (Heteroptera). Am. Mus. Novitates no. 1918, 15 pp.
- Ruckes, H. 1959a. Three new species of *Mecistorhinus* Dallas (Heteroptera, Pentatomidae). Am. Mus. Novitates no. 1930, 8 pp.
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## REVISION OF THE PLATYNINE CARABID GENUS *TANYSTOMA* MOTSCHULSKY (COLEOPTERA)

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**Abstract.**—The genus *Tanystoma* Motschulsky is revised, with a key to species, synonymies, and descriptions provided for *T. maculicolle* (Dejean), new combination, *T. cuyama*, new species, *T. striata* (Dejean), and *T. sulcata* (Dejean). Lectotypes are designated for the Dejean species. The cladistic relationships of *Tanystoma* are analyzed, and speciation events within the clade are attributed to Pleistocene oscillations of California grassland-chaparral. The vicariance pattern hypothesized for *Tanystoma* is compared to that exhibited by other groups of plants and animals and is found to represent a general pattern. This pattern entails sequential south to north vicariant events; the first isolating the Southern Coastal and Peninsular mountain ranges in California from coastal areas north of Monterey; the second event separating coastal mountain habitats in the Northern Coastal range of California from those in Oregon.

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The tule beetle, *Tanystoma maculicolle* (Dejean) is an extremely common ground beetle of California and southern Oregon. It has been variously named the overflow bug (Riley, 1882), stink bug, grease bug, or tule beetle (Essig, 1926; Anderson, 1975). Whereas this species commonly enters homes in agricultural areas, and has often become a nuisance during summer flights in the Central Valley, several related species are poorly known. These species differ from *T. maculicolle* by being exclusively brachypterous, and by possessing more restricted distributions in California and Oregon. All species are characterized by adaptation to the Mediterranean climate of California, where they live in grassland and chaparral habitats.

This paper presents a systematic study of *Tanystoma* Motschulsky. Recognition of *Tanystoma* as a distinct generic entity has been proposed recently (Liebherr, in press). *Tanystoma* is hypothesized to be the sister group of *Rhadine* LeConte, a genus comprised of predominantly subterranean and cave-inhabiting species. To facilitate recognition of *Tanystoma* species a key is provided to distinguish species of *Tanystoma* from other North American Platynini. Based on hypotheses of relationship in my classification of North American Platynini, the relationships of *Tanystoma* to other platynine genera are discussed. All species are described, with a key to species, synonymies, illustrations, and distributional maps included. What is known of the life histories and ecological preferences is presented. The descriptive taxonomy of the group is used as the basis for hypotheses of evolutionary relationships of the species. These hypotheses, based on cladistic criteria, are used in conjunction with the present-day distributions of the species to investigate the likely mechanisms that caused differentiation within the group.

### MATERIALS AND METHODS

**Material.** This study is based upon examination of 1,798 specimens of *Tanystoma*. I thank the following curators and institutions for lending material:

Lee H. Herman, American Museum of Natural History (AMNH);  
Nigel Stork, British Museum (Natural History) (BMNH);  
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*Methods.* Specimens were examined using a quartz halogen fibre optics ring light, and Zeiss dissecting microscope, from magnifications of  $8\times$  to  $125\times$ . When small or hidden structures were to be viewed, specimens were cleared in lactic acid, and then dissected. Slide mounts of mouthparts were made in glycerin jelly. Genitalic preparations were made by boiling specimens in soapy distilled water, followed by dissection. For males, the aedeagus and associated sclerites were removed, placed in cold 10% KOH overnight, and dissected. The aedeagal internal sac was everted using honed minutens while in the KOH. Subsequently the dissections were placed in dilute acetic acid and stored in microvials partially filled with glycerin. For females, the entire abdomen was removed from the specimen and placed in cold 10% KOH overnight. The tergites were removed and the gonocoxae and inverted apical sternites and tergite removed. To facilitate viewing, dissections were placed in a Chlorazol Black E suspension in 70% alcohol, after acidification with dilute acetic acid. Subsequently, abdominal tergites and sternites, and genitalic preparations were stored in microvials partially filled with glycerin.

Flight wing development varies in this group. As a correlate of that, the metathorax is shorter in brachypterous specimens. To quantify metathoracic development, the metepisterna of specimens, from samples representing all species, were measured using a camera lucida. Specimens were placed in a rotating specimen holder so that the metepisternum was horizontal in the microscope field of view. The four corners of the sclerite were marked on a piece of paper placed under the drawing tube, with the 3 measurements indicated in Figure 15 made with a mm rule and protractor. The ratio, inner margin length/transverse width (c/a of Fig. 15) maximally distinguished macropterous and brachypterous *T. maculicolle*. This ratio was recorded for all species, with a frequency histogram (Fig. 19) used as a means to present the data. As the ratio used is a relative measurement, specimen height on the microscope stage

did not matter. Female and male specimens were measured, and as there was no difference in metepisternal proportions between the sexes, the results from both sexes were pooled.

#### CLASSIFICATION

##### *Tanystoma* Motschulsky

*Tanystoma* Motschulsky, 1845:341.

*Tanystola* Motschulsky, 1850:69 (unjustified emendation due to recognition of the manuscript name, *Tanystoma* Eschscholtz [Diptera], as validly published); Motschulsky, 1864:317; Casey, 1920:4, 20.

*Leucagonum* Casey, 1920:99.

*Nomenclatural history.* The name *Tanystoma* was first proposed by Latreille (1816) as a "famille" level taxon of Diptera (C. Sabrosky, pers. comm.). Motschulsky proposed *Tanystoma* as a genus in 1845, with *T. striata* as the type species. In 1850, Motschulsky emended his *Tanystoma* to *Tanystola*, based on what he considered a prior generic usage of *Tanystoma* by Eschscholtz. Eschscholtz's *Tanystoma* remains a manuscript name (Neave, 1939), making Motschulsky's 1850 emendation unjustifiable. Even though *Tanystola* has remained in use since 1850, either as a distinct genus (Casey, 1920), or as a subgenus of *Agonum* (Hatch, 1951), the frequency of usage does not justify suppression of the older *Tanystoma* Motschulsky 1845.

*Diagnosis.* Distinguished from other Platynini by the diagnostic combination: antennae with 4 or more longer setae near apex of pedicel, shorter, very fine setae over surface of scape, pedicel and third segment (Figs. 7, 16); mentum with anteromedial setae close together, adjacent to anterior marginal bead (Fig. 6); pronotum with basal margin expanded posteriorly just inside hind angles; elytra with from 3–7 (usually from 4–6) dorsal setae; mesocoxae with a single seta on coxal ridge; tarsi with well developed outer longitudinal sulcus, weakly developed inner sulcus; body surface with sparse very fine setation (Figs. 17, 18).

The following key is modified from a fully resolved key to North American Platynini (Liebherr, in press) and permits separation of *Tanystoma* from other platynine genera. The key makes extensive use of genitalic and reproductive tract characters, making it difficult to use. However, its presentation here provides a view to the types of characters necessary to diagnose genera of Platynini.

#### KEY TO PLATYNINI OF NORTH AMERICA

- 1(0). Mentum without tooth, spermathecal duct short and cuplike, sclerotized, entering on median oviduct ..... *Olisthopus* Dejean
- 1'. Mentum with variously developed median tooth, spermatheca ovoid to elongate, duct not heavily sclerotized ..... 2
- 2(1). Claws variously pectinate ..... 3
- 2'. Claws smooth, not pectinate ..... 4
- 3(2). Claws chelate, tarsi of both sexes with numerous flattened setae on undersides of first 4 tarsal segments ..... *Onypterygia* Dejean
- 3'. Claws normal, not chelate, mid- and hindtarsi with only lateral rows of spines beneath ..... *Pristonychus* Dejean, *Calathus* Bonelli, *Synuchus* Gyllenhal

4(2).	Outer surface of foretibia with median canalicula, plus fore and hind grooves . . .	<i>Glyptolenus</i> Bates
4'.	Outer surface of foretibia without median groove, fore and hind grooves present	5
5(4).	Male genitalia with apical setae on parameres . . . . .	<i>Sericoda</i> Kirby, <i>Elliptoleus</i> Bates
5'.	Male genitalia with glabrous parameres . . . . .	6
6(5).	Median sulcus well developed on metatarsi . . . . .	<i>Agonum</i> Bonelli (in part), <i>Pseudanchus</i> Casey, <i>Paranchus</i> Lindroth, <i>Rhadine</i> LeConte (in part)
6'.	Median sulcus absent or only faintly visible on metatarsi . . . . .	7
7(6).	Posterior lateral pronotal seta absent . . . . .	<i>Rhadine</i> LeConte (in part), <i>Agonum</i> Bonelli (in part), <i>Anchomenus</i> Bonelli
7'.	Posterior lateral pronotal seta present . . . . .	8
8(7).	Spines or heavy spicular fields present on internal sac of aedeagus . . . . .	9
8'.	Aedeagal sac without heavy spines or fields of spicules . . . . .	11
9(8).	Neck constricted . . . . .	<i>Platynus</i> Bonelli (in part), <i>Rhadine</i> LeConte (in part)
9'.	Neck not constricted . . . . .	10
10(9).	Four or more setae at apex of 2nd antennal segment . . . . .	<i>Tanystoma</i> Motschulsky
10'.	Fewer than 4 setae near apex of 2nd antennal segment . . . . .	<i>Agonum</i> Bonelli (in part)
11(8).	Neck constricted; fine pubescence covering body surface . . . . .	<i>Atranus</i> LeConte, <i>Anchus</i> LeConte
11'.	Neck constricted or not; if constricted, body glabrous . . . . .	<i>Agonum</i> Ponelli (in part), <i>Platynus</i> Bonelli (in part)

The natural affinities of the platynine genera are best inferred using shared derived character states of the male and female reproductive tract. The generalized external anatomy of Platynini precludes construction of a phylogenetic classification using only external characters. Based on shared derived states of characters in the female reproductive tract and the male aedeagus, *Tanystoma* is the sister genus to *Rhadine* in the subtribe Platynina (Liebherr, in press). *Tanystoma* and *Rhadine* share a similar derived spermathecal configuration, with the spermatheca angulate near its base (Figs. 23, 24, 28, 32). Many *Rhadine* species possess fields of flattened spines on the aedeagal internal sac, similar to the condition in *Tanystoma cuyama*, *T. striata* and *T. sulcata*. In addition, the pronotum of *Tanystoma* species is similar to the trisinate pronotum of *Rhadine*, a point noted by Hatch (1951, p. 118). All *Tanystoma* and most *Rhadine* species possess sparse pubescence which can be seen on antennal segments 1–3, and on portions of the body where the beetle’s activity has not rubbed it off (Figs. 17, 18). *Tanystoma* is distinguished from *Rhadine* by the derived state of at least 4 longer setae near the apex of the pedicel of the antenna. The larva of *T. maculicolle* possesses the derived state of segmented urogomphi (Liebherr, 1984), but the distribution of this feature among other *Tanystoma* and *Rhadine* is unknown.

*Description.* Body form *Agonum*-like, head and pronotum broad; lateral areas of pronotal hind margin expanded posteriorly; elytra oviform to parallel sided; length from apex of labrum to elytral tip, 5.9–9.1 mm. Head with frons and vertex convex, wrinkled mesal to eye margin; labrum quadrate, sides angled somewhat to meet front margin, 6 large setae along front margin, about 24 small setae each side along lateral edge and on underside (Fig. 1); mandibles relatively stout; right mandible with anterior retinacular tooth mesally on inner surface (Fig. 2); weakly developed terebral tooth, posterior retinacular tooth, and premolar tooth; left mandible without anterior



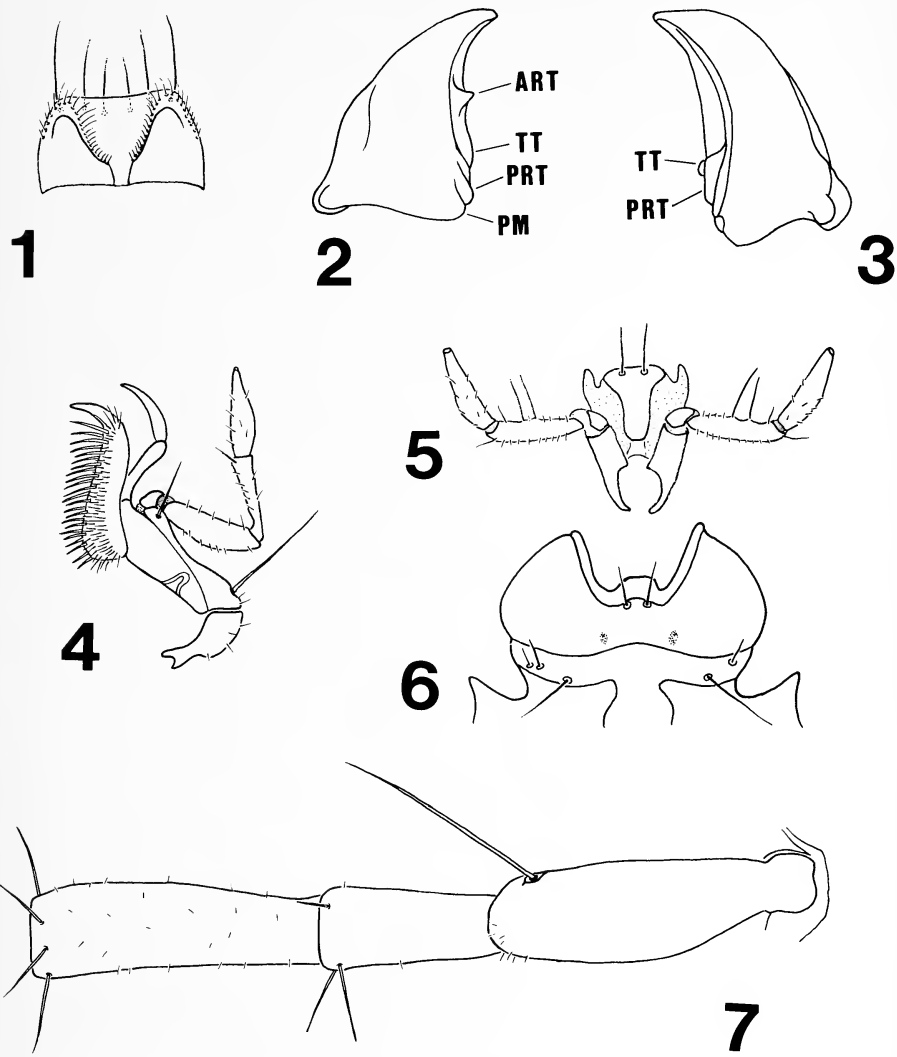
retinacular tooth, with terebral, posterior retinacular, and premolar teeth present (Fig. 3); maxilla with very finely setose 3-segmented palp, lacinia with thick brush-like setae, galea glabrous (Fig. 4); labrum with membranous paraglossae, ligula bisetose with thick fore margin, labial palps with 2 larger setae on fore margin of penultimate segment, penultimate and apical palpal segments subequal (Fig. 5); mentum with unidentate anterior margin, tooth triangular to subtruncate (Fig. 6), mentum bisetose with setae close together, just posterad of marginal bead, foveae of mentum well developed, circular; submentum usually with 2, occasionally with 3, setae on a side (Fig. 6); antennal segment 1 with single long seta on outer surface near apex (Fig. 7), segment 2 with at least 4 longer setae near apex, segment 3 with apical ring of 6 setae, segments 1 to 3 with very fine setae in addition to longer apical setae, segments 4–11 with fine pubescence over entire surface, and apical ring of setae (Fig. 16). Pronotum with posteriorly expanded laterobasal margins (Figs. 8–11), lateral margins convex to slightly sinuate basally; flight wings present or absent, metathoracic development correlated with development of flight wings, metepisternum elongate to quadrate (Figs. 12–15, 19). Elytra oviform to parallel sided at middle, humeral development correlated with flight wing development; 4–7 (rarely 3) dorsal setae in or adjacent to third elytral interval; 14–18 umbilicate setiferous punctures in eighth elytral stria. Legs moderately robust to slender; mesocoxa with single seta on ridge adjacent to trochanter; tarsi with evident external sulcus and weakly developed internal sulcus; unguis setose, bearing 8 ventrolateral setae; claws smooth. Male genitalia with parameres subequal, rounded, with glabrous apices; median lobe lightly pigmented, evenly curved except in the smallest *T. maculicolle* specimens; internal sac either with spicules over much of the surface (Figs. 20, 21), or with patch of stout spines (Figs. 22, 29, 31). Female genitalia with gonocoxae two-segmented, basal segment with fringe of 6 to 19 setae, apical segment moderately pointed, bearing 2 lateral and one dorsal ensiform setae, and 2 nematiform setae set in an apical pit (Figs. 23, 24, 28, 32); bursa copulatrix membranous, with a lateral expansion on the right side; spermatheca elongate and angulate near the base, irregularly constricted, attached to bursa near entrance of median oviduct; spermathecal gland connected to angled portion of spermatheca by a moderately long duct (Figs. 23, 24, 28, 32). Vertex of head, lateral and basal areas of pronotum, elytra and ventral body surface with isodiametric microsculpture; disc of pronotum with microsculpture stretched to form transverse mesh; entire body surface covered with variably evident pelage of very fine erect setae (Figs. 16–18), setation not as evident on disc of pronotum and elytra due to wear of specimens.

*Larval stages.* The larva of *T. maculicolle* (Liebherr, 1984) possesses an inner lobe on the maxilla and a cervical keel, characters shared with other Platynini. The urogomphi of *T. maculicolle* larvae are segmented, and of a configuration similar to that observed in *Cymindis* (Hürka, 1969).

*Type species.* *T. striata* (Dejean), designated by Motschulsky (1845).

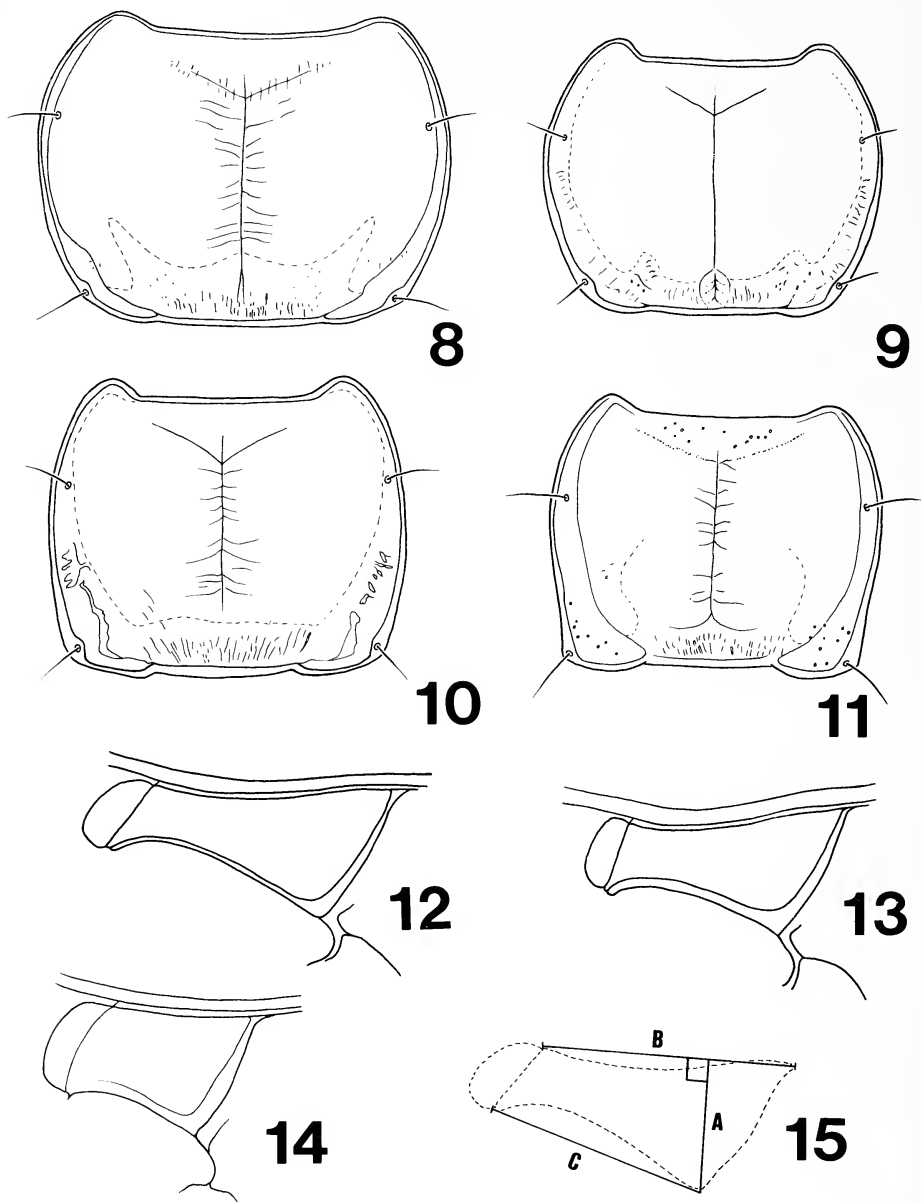
#### KEY TO ADULTS OF *Tanystoma* MOTSCHULSKY

- |     |   |   |
|-----|---|---|
| 1.  | Body with lateral edges testaceous, center of pronotum and elytra brunneous to piceous; legs testaceous ..... | 2 |
| 1'. | Body unicolorous, brunneous to piceous; legs brunneous .....  | 3 |

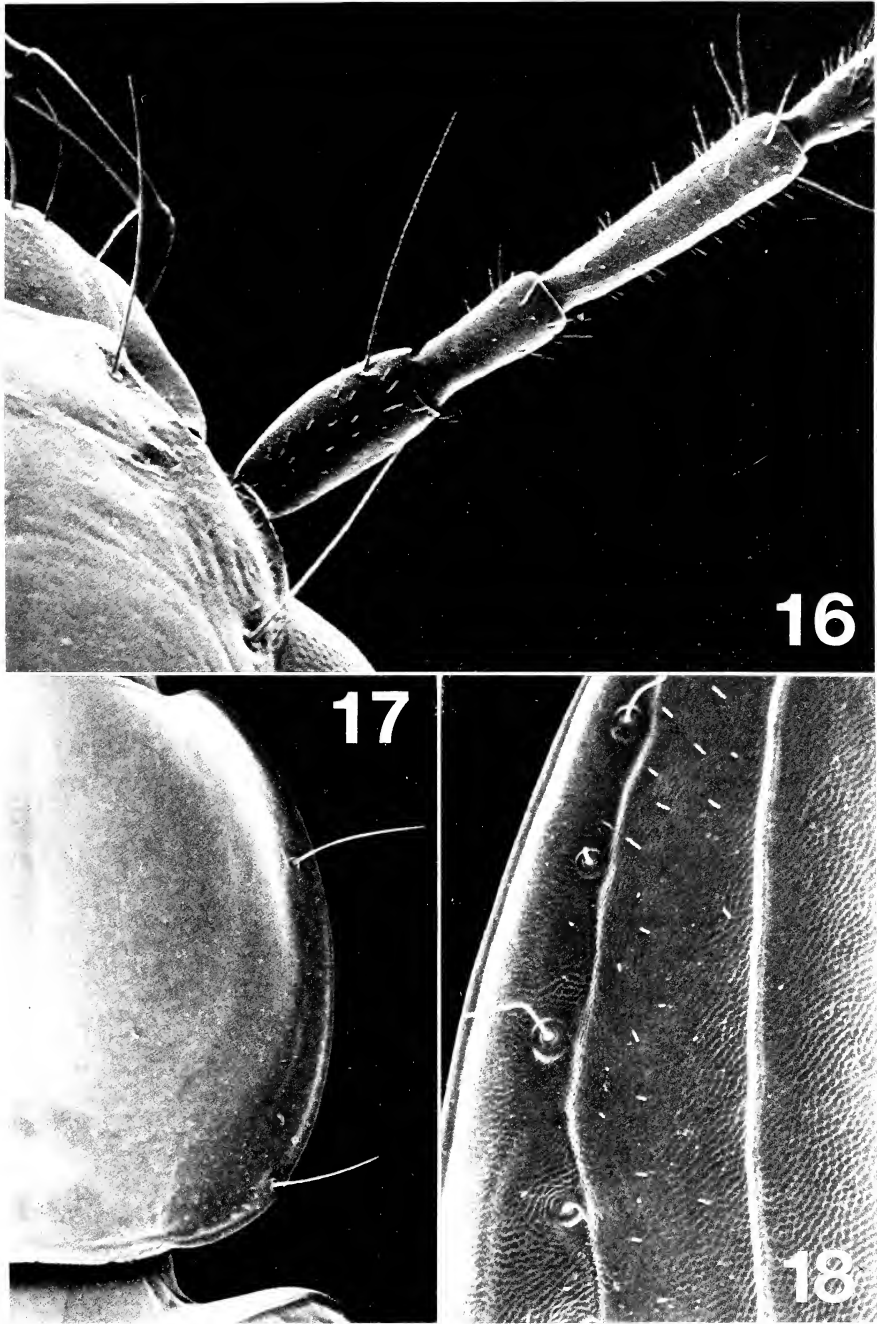


Figs. 1-7. *Tanystoma maculicolle*. 1. Labrum, ventral view. 2. Right mandible, ventral view (ART = anterior retinacular tooth; TT = terebral tooth; PRT = posterior retinacular tooth; PM = premolar tooth). 3. Left mandible, ventral view (same abbreviations). 4. Left maxilla, ventral view. 5. Labium, ventral view. 6. Mentum and submentum, ventral view. 7. *T. striata*, scape, pedicel, first flagellomere of antenna, outer lateral view.

2(1). Median portion of elytra with central dark area expanded laterally to 6th stria; in basal  $\frac{1}{4}$  and apical  $\frac{1}{8}$ , dark area expanded to vicinity of the 4th stria; expansion of piceous area from 4th to 6th stria abrupt; flight wings dimorphic, either fully developed or vestigial ..... *T. maculicolle* (Dej.)



Figs. 8-15. 8. *T. maculicollis* pronotum. 9. *T. cuyama* pronotum. 10. *T. striata* pronotum. 11. *T. sulcata* pronotum. 12. *T. maculicollis* right metepisternum and metepimeron, winged specimen. 13. *T. maculicollis* right metepisternum and metepimeron, brachypterous specimen. 14. *T. sulcata*, right metepisternum and metepimeron. 15. Measurements made on metepisterna (A = transverse width; B = outer margin length; C = inner margin length).



Figs. 16–18. Scanning electron micrographs of *T. maculicolle*. 16. Right antenna (dorsal view, 50 $\times$ ). 17. Right half of pronotum (31 $\times$ ). 18. Humeral margin of left elytron (92 $\times$ ).

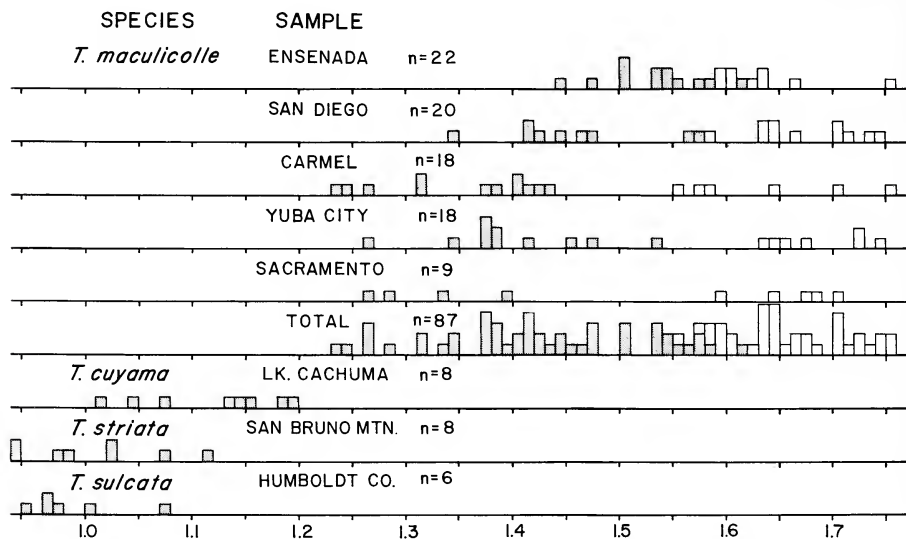


Fig. 19. Frequency distribution of the ratio  $c/a$ , inner margin length of metepisternum/transverse width of metepisternum, for species of *Tanystoma*. For *T. maculicolle*, stippled bars represent brachypterous individuals, open bars represent fully winged individuals. Vertical scale such that square areas represent one individual,  $n$  = sample size.

- 2'. Elytra with central dark area evenly bordered, interval 8 and 9 progressively more testaceous approaching lateral margin; humeri becoming gradually lighter laterally; brachypterous ..... *T. cuyama*, new species
- 3(1). Hind margin of pronotum strongly expanded posteriorly; pronotal hind angle evident; lateral margin sinuate before basal seta (Fig. 11), notch often present in marginal bead laterad basal seta (Fig. 30) ..... *T. sulcata* (Dej.)
- 3'. Hind margin of pronotum moderately expanded posteriorly; pronotal hind angle rounded; lateral margin convex to straight before basal seta, marginal bead without notch near basal seta (Fig. 10). ..... *T. striata* (Dej.)

#### *Tanystoma maculicolle* (Dejean), New Combination

*Agonum maculicolle* Dejean, 1828:175.

*Anchomenus maculicollis*, Mannerheim, 1843:199.

*Platynus maculicollis*, LeConte, 1854:55.

*Agonum* (*Leucagonum*) *maculicolle*, Casey, 1920:100.

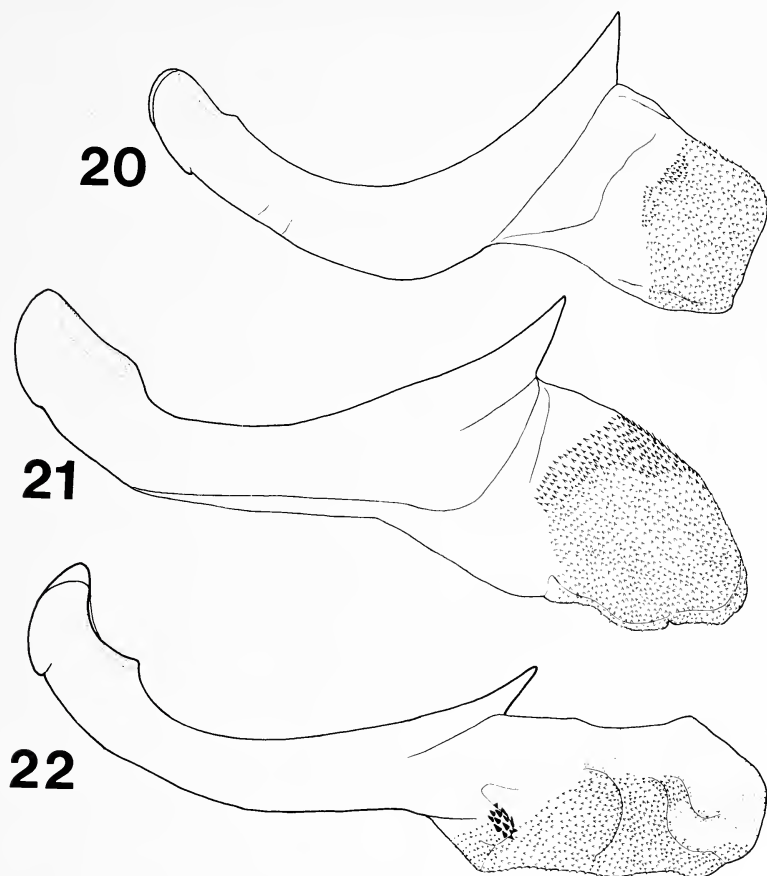
*Agonum* (*Leucagonum*) *maculicolle guadelupense* Casey, 1920:100.

*Agonum* (*Leucagonum*) *angustior* Casey, 1920:101. **New Synonymy.**

*Tanystoma maculicolle*, Liebherr, 1984:531.

**Diagnosis.** Center of pronotum piceous, contrasting with testaceous lateral borders; elytral intervals 2, 3, and 4 piceous from base to apical  $\frac{1}{8}$ , intervals 5 and 6 piceous between  $\frac{1}{8}$  and  $\frac{5}{8}$  of length of elytra, intervals 7–9 testaceous to brunneous; flight





Figs. 20–22. Median lobe of aedeagus (lateral view). 20. *T. maculicolle*, CA: Los Angeles Co., San Clemente Isl. 21. *T. maculicolle*, CA: Calaveras Co., West Point. 22. *T. cuyama*, CA: Sta. Barbara Co., Lk. Cachuma.

wings dimorphic, either fully developed or a vestigial flap; metepisternum elongate (Figs. 12, 13); internal sac of male aedeagus lacking patch of stout spines.

*Description.* Head with eyes relatively flat, not produced laterally, temples outwardly expanded to meet hind margin of eye; mentum with deep, rounded foveolar pits (Fig. 6); scape, pedicel and third antennal segment with numerous erect setae over length of segments in addition to larger apical setae (Fig. 16). Pronotum with hind angles barely indicated, nearly round; lateral margins of base slightly convex posteriorly (Fig. 8); laterobasal depressions evenly contoured from basal and lateral margins to elevation of disc; disc convex, lateral areas depressed; laterobasal depressions narrowed near middle of lateral margin; lateral depressions narrowed evenly in front of lateral setae to front angles; front angles rounded, not strongly produced;



Figs. 23, 24. Female reproductive tract (ventral view); see text for explanation. 23. *T. maculicollis*, CA: Sta. Clara Co., Lk. Lagunitas. 24. *T. cuyama*, CA: Monterey Co., Carmel.

anterior marginal bead evident medially; median longitudinal impression fine, intersected by numerous wrinkles; anterior transverse impressions weakly developed, traversed by weak longitudinal wrinkles; base of pronotum with very fine longitudinal wrinkles medially; basal marginal bead broad, more clearly demarked just inside laterobasal depressions. Elytra parallel sided, at least in median  $\frac{1}{3}$ ; humeri broad, humeral angles rounded due to lateral expansion of elytral margins behind humerus; dorsal surface moderately convex; 14 to 17 lateral umbilicate setiferous punctures in eighth elytral stria; 4 to 7 dorsal setae in or adjacent to third interval; elytral intervals moderately convex, elytral striae well defined. Metathoracic development and wing length dimorphic; wings either fully developed or vestigial membranous flaps; if macropterous, inner lateral length of metepisternum  $1.55\text{--}1.76 \times$  transverse width (Figs. 12, 15, 19), if brachypterous, lateral length of metepisternum  $1.24\text{--}1.62 \times$  transverse width (Figs. 13, 15, 19); scutellum convex, slightly elevated above level of scutellar striole. Legs moderately elongate (as in Fig. 26). Male genitalia with median lobe of aedeagus unevenly curved (Fig. 21), more angled in smaller specimens (Fig. 20); internal sac with spicules over much of the surface. Female genitalia with basal segment of gonocoxae bearing fringe of from 8 to 19 setae (Fig. 23), difference in number of setae from left to right side averaging 1.5 ( $s = 1.1$ ,  $N = 24$ ); fine setae along outer surface of tergum X, setae sparsely distributed on membrane dorsal to gonocoxal bases; spermatheca angulate, elongate, somewhat

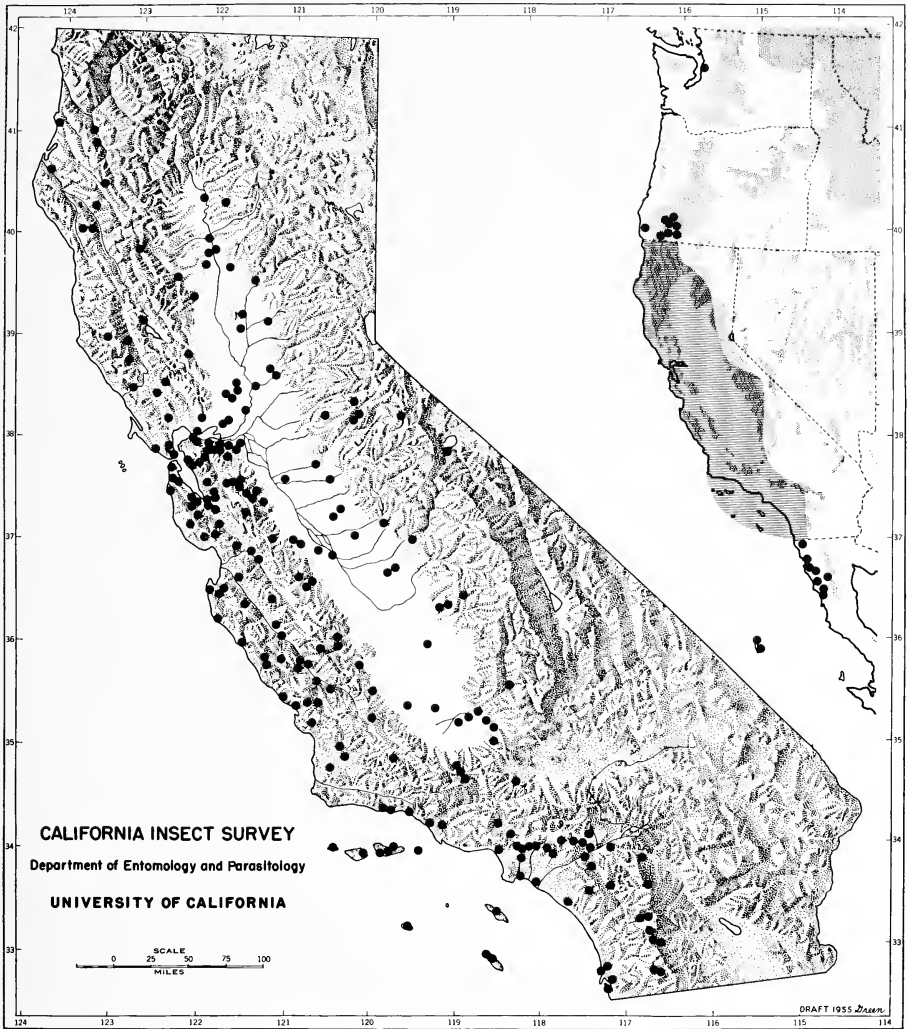


Fig. 25. Distribution of *T. maculicollis*; inset shows distribution outside California. Introductions in Hawaii and New York not shown.

inflated medially. Body surface with very fine setae, evidenced by fine punctulations (Figs. 17, 18); microsculpture on vertex of head isodiametric; pronotal disc with laterally stretched isodiametric microsculpture, approaching a transverse mesh in some places; latero-basal depressions and base of pronotum with irregular, wavy isodiametric meshes; elytra with isodiametric microsculpture, cells sometimes lined up in transverse rows, microsculpture punctuated by punctulations associated with fine secondary pubescence. 5.9 mm (♂, San Clemente Isl.)–9.1 mm (♀, Santa Rosa Isl.).

*Types.* Of *maculicolle*, male lectotype hereby designated, green sex label, type locality Santa Barbara, California, hereby designated (MHNP); of *guadelupense*, female holotype, Guadalupe Island, Mexico, Baja California del Norte (USNM); of *angustior*, male holotype, Hoopa Valley, Humboldt Co., California (USNM).

*Distribution.* Found throughout cismontane California, coastal Baja California del Norte, and southwestern Oregon (Fig. 25), the California Channel Islands, and Guadalupe Island, Baja California. Apparently introduced and possibly established at Seattle, Washington. Introduced, with establishment unknown at Honolulu, Hawaii (1 specimen, USNM), and New York City (1 specimen, CAS).

*Material examined.* This is an extremely common species in California, and I have foregone listing localities for all of the 1,641 specimens examined from that state. Records from the margin of the species range and from introductions follow. **MEX:** BAJA CAL. NORTE: Agua Caliente (1, CAS); Colnett (1, CAS); Colonia Guerrero (1, CISC); Ensenada (16, CAS); Guadalupe Isl. (5, CAS); Hamilton Ranch (1, CAS); Las Cabras (6, CAS); Maneadero (24, CAS). **U.S.A.:** CA: *Mono Co.:* Mono Lk., Borax Lk. (1, CAS). OR: *Curry Co.:* Pistol River (1, ORSU). *Jackson Co.:* Copper (1, ORSU); Gold Hill (3, ORSU); Jacksonville (2, AMNH); Medford (1, AMNH; 2, ORSU); Sam's Valley (1, AMNH); Wimer (1, ORSU). *Josephine Co.:* Grayback Ck. W Oregon Caves (1, ORSU). WA: Seattle, 23-IV-1912 (1, ORSU); "in backyard" (brachypterous), 11-VI-1940 (1, ORSU).

### ***Tanystoma cuyama*, new species**

*Diagnosis.* Head, center of pronotum, and elytra brunneous; lateral edges of pronotum and elytra, and legs testaceous; pronotum with hind angles evenly rounded, not strongly produced posterad; apterous, metepisternum with lateral and anterior edges subequal; internal sac of male aedeagus with from 15 to 30 large spines in a patch (Fig. 22).

*Description.* Head with eyes moderately convex, temple expanded slightly to meet hind margin of eye (Fig. 26); mentum with rounded to triangular tooth; foveolar pits of mentum well developed, rounded; scape, pedicel and third segment covered with short erect setae in addition to larger apical setae. Pronotum with lateral margin of base moderately expanded posteriorly (Fig. 9); lateral margins convex, slightly reflexed before hind lateral setae; lateral depressions narrowed to area of anterior lateral setae, only slightly narrower to anterior pronotal angles; anterior angles somewhat produced, rounded; anterior marginal bead evident; median longitudinal impression and anterior transverse impressions weakly developed, median impression widened toward posterior margin of pronotum; base of pronotum with weakly developed longitudinal wrinkles, some deeper laterally, suggestive of poorly developed punctulae; posterior marginal bead evident across median portion of trisinate margin. Elytra oviform, sides evenly rounded, humeri approximately as broad as pronotum (Fig. 26); basal elytral grooves posteriorly convex, humeri subangulate, lateral margins evenly convex outside of humeral angles; dorsal surface convex, curving ventrally toward apex of elytra; 15–18 lateral umbilicate setiferous punctures in eighth elytral stria, 4 to 6 dorsal setae in or adjacent to third interval; dorsal setation somewhat unstable, with setae occasionally present in or adjacent to second interval (Fig. 26); elytral intervals nearly flat, striae shallow, their sides gently sloping. Metathorax shorter than in winged species, length of interior margin of metepisternum 1.0–1.2 ×

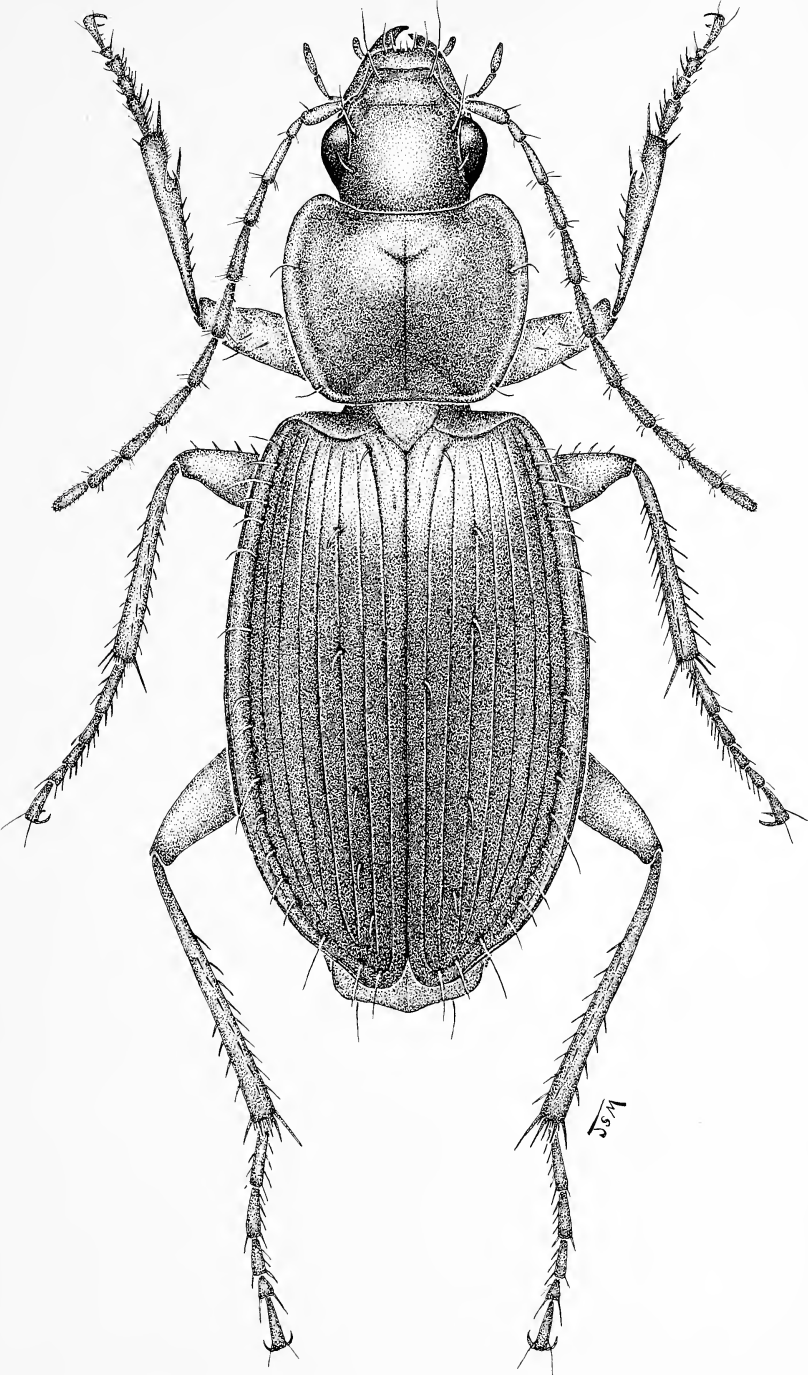


Fig. 26. Male paratype of *T. cuyama*, new species; CA: Sta. Barbara Co., Lk. Cachuma.



transverse width (Figs. 15, 19); scutellum large, triangular and flat (Fig. 26). Legs moderately elongate (Fig. 26). Male genitalia with median lobe of aedeagus slender, evenly curved (Fig. 22); internal sac with spicules over much of the surface, spiny patch of from 15–30 spines ( $N = 7$ ) near base of sac. Female genitalia with basal segment of gonocoxae bearing fringe of from 7 to 14 setae (Fig. 24), difference in number of setae from left to right side averaging 1.6 ( $s = 1.7$ ,  $N = 11$ ); fine setae on membranous dorsal surface of genital chamber; spermatheca angulate and elongate. Body surface sparsely covered with very small setae (as in Fig. 18), best viewed obliquely at high magnification, often rubbed off pronotal and elytral discs, more often visible along depressed pronotal and elytral margins, and on ventral body surface; microsculpture on vertex of head isodiametric, weakly developed; pronotal disc with laterally stretched transverse mesh, like a matrix of bricks in appearance; lateral depressions and base of pronotum with irregular isodiametric microsculpture; scutellum and elytra with well developed isodiametric microsculpture, granulate in appearance. 6.1–8.2 mm.

*Holotype*. Male, CA: Santa Barbara Co., Lk. Cachuma, Hwy. 54, 18 mi SE Hwy. 101, 4-XII-1981, elev. 800', J. K. Liebherr (CUIC).

*Allotype*. Female, CA: Monterey Co., Pfeiffer State Park, 3-VI-1981, D. L. Wagner (CISC).

*Etymology*. Named to honor the memory of the Cuyama Indians, who inhabited the coastal areas near Santa Barbara.

*Distribution*. Found in the Coast Ranges of California, from Carmel on the north, to San Ysidro on the south (Fig. 27). An apparent gap in the distribution occurs in and around the Los Angeles Basin.

*Paratypes* (86). U.S.A.: CA: no other data (2♂♂, MCZ). *Monterey Co.*: Big Sur, 21-I-1934 (1♂, CAS), 9-I-1939 (4♂♂, CAS); Carmel, 4-I-1907 (1♀, CAS), 9-VI-1908 (1♀, CAS), 12-II-1911 (5♀♀, CAS), 9-IV-1911 (1♂, CAS), 17-XII-1916 (1♀, CAS), 23-III-1919 (3♂♂, 4♀♀, CAS), 24-III-1919 (3♂♂, 2♀♀, CAS), 4-VIII-1919 (1♂, CAS), 25-XII-1919 (1♂, CAS), 4-XII-1921 (4♂♂, 1♀, CAS), 9-IV-1922 (2♀♀, CUIC), 9-I-1939 (1♂, CAS), 22-XI-1969 (1♂, CISC); Pfeiffer S. P., 3-VI-1981 (1♂, CISC); Tassajara Hot Spgs., 15-X-1908 (1♀, CAS), 17-X-1908 (1♂, CAS). *San Luis Obispo Co.*: Cambria, 19-V-1930 (1♂, CAS), 8-I-1939 (1♂, 2♀♀, CAS). *Sta. Barbara Co.*: Lk. Cachuma, Hwy. 54, 18 mi SE Hwy. 101, 4-XII-1981, elev. 800' (5♂♂, 2♀♀, CUIC; 8♂♂, 8♀♀, CAS); San Marcos Fire Sta., 2,200' elev. 21-II-1971 (3♂♂, 2♀♀, CISC); Santa Barbara, 5-I-1923 (1♂, 2♀♀, MCZ), 26-XI-1928 (1♂, CAS), 22-XII-1928 (2♂♂, 1♀, CAS). *Riverside Co.*: San Jacinto Mtns., 1932 (1♂, CAS). *San Diego Co.*: Poway (1♂, 2♀♀, CAS); San Ysidro, 25-XII-1910, 500' elev. (1♂, MCZ).

### *Tanystoma striata* (Dejean)

*Anchomenus striatus* Dejean, 1828:132.

*Tanystoma striata*, Motschulsky, 1845:341.

*Tanystola striata*, Motschulsky, 1850:69, 1864:317; Casey, 1920:21.

*Agonum (Batenus) striatum*, Csiki, 1931:851.

*Agonum (Tanystola) striatum*, Hatch, 1951:119.

*Diagnosis*. Body color uniform brunneus to piceous; pronotal hind margin with

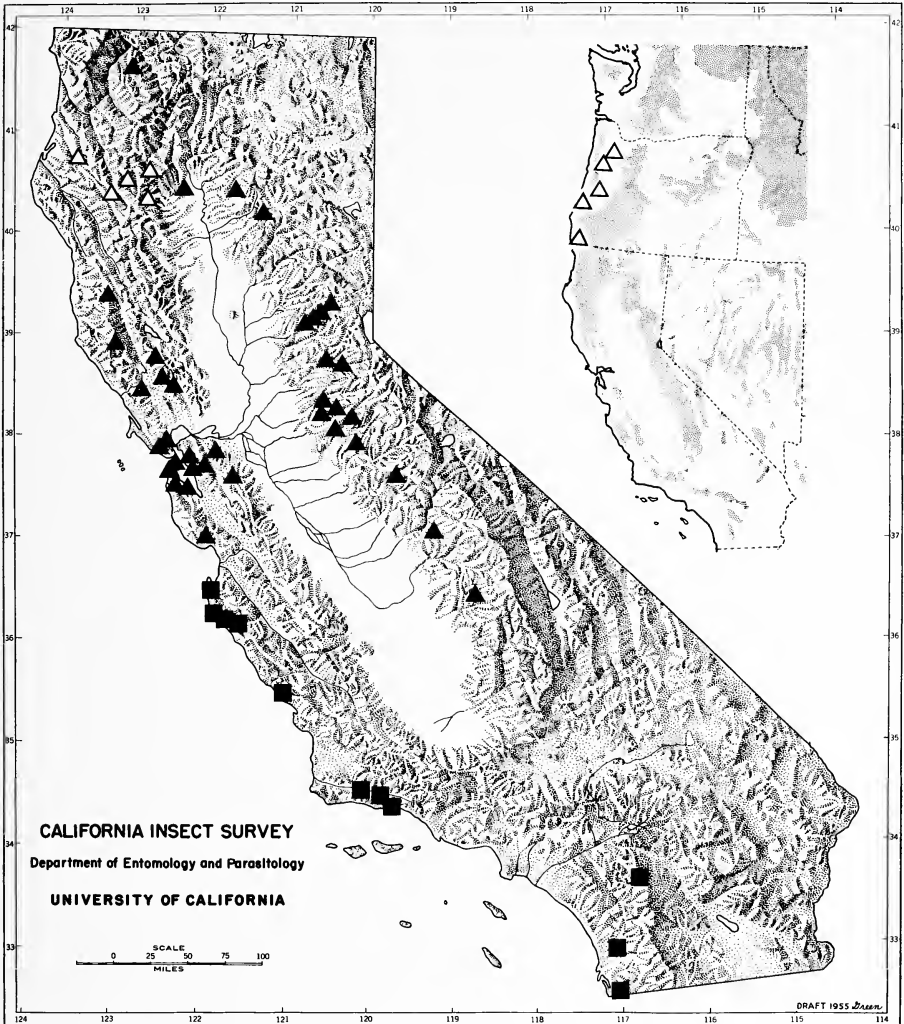


Fig. 27. Distribution of *T. cuyama*, new species (squares); *T. striata* (solid triangles); *T. sulcata* (open triangles); inset shows distribution outside California.

lateral areas moderately produced posteriorly, hind angles rounded, lateral margins before hind angles convex (Fig. 10); apterous, metepisternum quadrate.

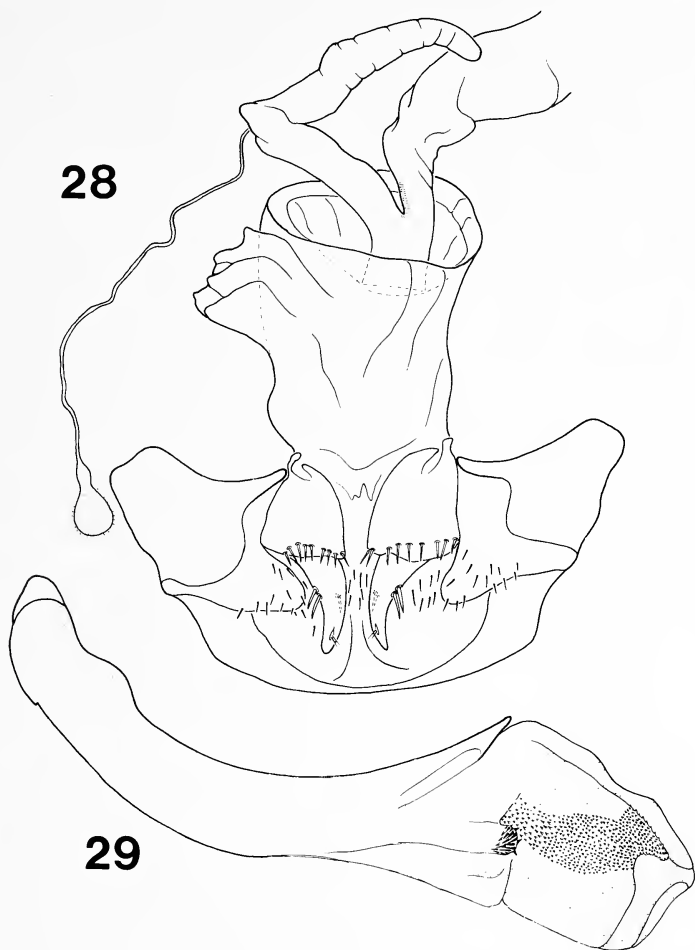
*Description.* Head broad; eyes moderately convex; temples expanded to meet hind margin of eye; tooth of mentum variable, sharply triangular to subtruncate; foveolar pits of mentum rounded, well developed; scape, pedicel, and third antennal segment with fine setation in addition to apical setae (Fig. 7). Pronotum with hind angles rounded (Fig. 10); laterobasal depressions punctate inwardly in some individuals,

with rugose surface anterad in lateral depressions; basal marginal bead well developed; thickened in areas of hind setae; lateral marginal bead reflexed, thinner anterad to anterior setae, thin and less reflexed to front angles; lateral margin convex before hind angles, evenly curved; front angles moderately produced; anterior marginal bead evident across medial area of notum; median longitudinal impression evident, though weakly developed; anterior transverse impression well developed medially, evanescent laterally; median impression intersected by transverse wrinkles; base of pronotum with longitudinal wrinkles, basal bead broad, evident medially in most individuals. Elytra broad medially, sides somewhat straight at middle, curved evenly to humeri, apex broad, sutural angle rounded (but more angulate than in *T. sulcata*); humeral regions only slightly reflexed, basal groove moderately convex, humeral angle angulate; 16–18 umbilicate setiferous punctures in eighth elytral stria; 3 to 5 dorsal setae in or adjacent to third elytral interval; elytral intervals slightly convex, striae well developed. Metathorax shortened, length of interior margin of metepisternum  $0.94\text{--}1.15 \times$  transverse width (Figs. 15, 19); scutellum large, triangular. Leg with fore- and midfemora and tibiae robust; legs short relative to other body proportions. Male genitalia with median lobe of aedeagus evenly curved; internal sac with spicules over portions of the surface, spiny patch of 14–20 spines ( $N = 7$ ) near base of sac (Fig. 29). Female genitalia with basal segment of gonocoxae bearing setal fringe of from 6–12 setae (Fig. 28), difference in number of setae from left to right side averaging 1.2 ( $s = 1.2$ ,  $N = 16$ ); fine setae present on dorsal surface of genital chamber above gonocoxae; spermatheca angulate and elongate. Body surface with sparse, very fine pubescence (as in Fig. 18), best viewed obliquely at high magnification; setation less well developed than in *T. maculicollis* or *T. cuyama*, but evident on lateral depressions of pronotum and elytra, and on ventral body surface; vertex of head with well developed isodiametric microsculpture, transverse to oblique wrinkles often present medial to eye margins; pronotal disc with laterally stretched isodiametric microsculpture, base and lateral depressions with well developed isodiametric microsculpture, somewhat irregular due to rugose surface; scutellum and elytra with well developed isodiametric microsculpture; elytral surface shiny, somewhat alutaceous. 6.3–9.1 mm.

*Type.* Of *striata*, male lectotype hereby designated, green sex label, type locality San Bruno Mtn., San Mateo Co., California, hereby designated (MHNP).

*Distribution.* Coast Ranges of California from Santa Cruz and Alameda counties, north to Siskiyou County, and eastward in the western Sierra Nevada foothills, between Shasta and Tulare counties.

*Material examined.* U.S.A: CA: Santa Cruz Co.: Santa Cruz Mts. (1, CAS). San Mateo Co.: San Bruno Mtn. (14, JKL); San Mateo (4, CAS). San Francisco Co.: Lake Merced (1, CAS); Mission Hills (1, CAS); San Francisco (13, CAS). Alameda Co.: no other data (7, CAS); Berkeley (8, CUIC); Livermore (2, CAS); Oakland (3, CAS; 2, JKL). Contra Costa Co.: Mt. Diablo (30, CAS; 1, MCZ). Marin Co.: no other data (1, AMNH); Carson Ridge (1, CISC); Mt. Tamalpais (1, CAS); Ross (1, CAS). Sonoma Co. (1, CAS). Napa Co.: no other data (1, CAS); Calistoga (2, CAS); Mt. St. Helena (4, CAS). Lake Co.: Anderson Spgs. (1, CAS). Mendocino Co.: 5 mi N Willetts (1, CISC); Yorkville (1, CAS). Siskiyou Co.: no other data (3, ORSU); Lake Mtn. (1, CAS). Shasta Co.: no other data (5, CAS); Mts. E of Redding (3, CAS). Tehama Co.: Deer Ck. Meadow, Chico-Chester Rd. (2, CAS). Nevada Co.: Bear Valley (1, UCD).



Figs. 28, 29. *T. striata*. 28. Female reproductive tract (ventral view), CA: Napa Co., Mt. St. Helena. 29. Median lobe of aedeagus (lateral view); CA: Amador Co.

*Placer Co.*: Bear R. nr. Hwy. 20 (13, CAS); Dutch Flat (2, CUIC); Emigrant Gap (1, CISC). *El Dorado Co.*: Pacific House (3, CAS; 2, CNC); nr. Whitehall (2, LACM). *Amador Co.*: Pine Grove (1, CDFA). *Calaveras Co.*: Big Tree (1, CAS); Mokelumne Hill (3, CAS); Murphys (1, CAS); Railroad Flat (7, CAS). *Tuolumne Co.*: Twain Harte (1, CAS). *Mariposa Co.*: Yosemite (2, CAS). *Fresno Co.*: Shaver Lk. (1, CAS). *Tulare Co.*: Sequoia N.P. (1, CAS).

*Tanystoma sulcata* (Dejean)

*Anchomenus sulcatus* Dejean, 1828:131.

*Tanystola sulcata*, Motschulsky, 1850:70; Casey, 1920:21.

*Agonum (Batenus) sulcatum*, Csiki, 1931:851.

*Agonum (Tanystola) sulcatum*, Hatch, 1951:119.

*Agonum (Tanystola) charactum* Hatch, 1951:117. **New Synonymy.**

*Diagnosis.* Body color uniformly brunneous to piceous; pronotal hind margin with lateral areas strongly produced posteriorly, hind angles obtusely angulate (Figs. 11, 30); lateral margins often with notch outside hind lateral setae, margin straight or concave before hind angle; apterous, metepisternum quadrate.

*Description.* Head broad; eyes barely convex; temples expanded to meet hind margin of small eye; tooth of mentum obtuse angulate, triangular; foveolar pits of mentum rounded, well developed; scape, pedicel and third segment of antennae with fine setation in addition to apical setae. Pronotum with hind angles obtuse, rounded to angulate; lateral depressions with rugose surface, basal and lateral marginal beads thick, well developed; lateral margin straight (Fig. 30) to sinuate (Fig. 11) before hind angles, lateral margins often with notch laterad of hind setae (Fig. 30); lateral marginal depressions narrowed from laterobasal depressions to anterior pronotal setae, thereupon narrow to front angles; anterior pronotal angles rounded, weakly produced; anterior marginal bead weakly developed or absent medially; median longitudinal impression well developed, transverse anterior impressions almost obsolete; disc with transverse wrinkles; base of pronotal disc with well developed longitudinal wrinkles, basal bead poorly indicated or obsolete medially. Elytra broad, sides somewhat straightened at median of length, apex broad, sutural angles broadly rounded; humeral regions outwardly reflexed, basal groove moderately convex, humeral angle obtusely rounded-angulate; 14–17 umbiliculate setiferous punctures in eighth elytral stria; 3 to 5 dorsal setae in or adjacent to third elytral stria; elytral intervals slightly convex, striae well indicated. Metathorax shortened, length of interior margin of metepisternum  $0.95\text{--}1.1 \times$  transverse width (Figs. 14, 15, 19); scutellum large, triangular. Legs with fore- and midfemora and tibiae robust; legs short relative to other body proportions. Male genitalia with median lobe of aedeagus evenly curved; internal sac with spicules over much of the surface, spiny patch of 11–19 spines ( $N = 7$ ) near base of sac (Fig. 31). Female genitalia with basal segment of gonocoxae bearing fringe of from 7 to 12 setae (Fig. 32), difference in number of setae from left to right side averaging 1.0 ( $s = 0$ ;  $N = 5$ ); fine setae present on dorsal surface of genital chamber; spermatheca angulate and elongate. Body surface with sparse, very fine pubescence (as in Fig. 18), best viewed obliquely at high magnification; setation less well developed than in *T. maculicollis* and *T. cuyama*, but evident on lateral depressions of pronotum and elytra, and on ventral body surface; vertex of head with well developed isodiametric microsculpture, transverse to oblique wrinkles often present inside eye margins; pronotal disc with laterally stretched isodiametric microsculpture, base and lateral depressions with well developed isodiametric microsculpture; scutellum and elytra with well developed isodiametric microsculpture, elytral surface shiny, somewhat alutaceous. 6.0–8.1 mm.

*Types.* Of *sulcata*, female lectotype, green sex label, type locality Coos Bay, Oregon, hereby designated (MHNP); of *charactum*, holotype, Oregon, Coos Bay, 10-VIII, 1941 (USNM).

*Distribution.* Northern Coast Range of California, northeastern California, and western Oregon north to Marion Co. (Silverton). Old records (1890) list western Washington (Bowditch Coll., MCZ).



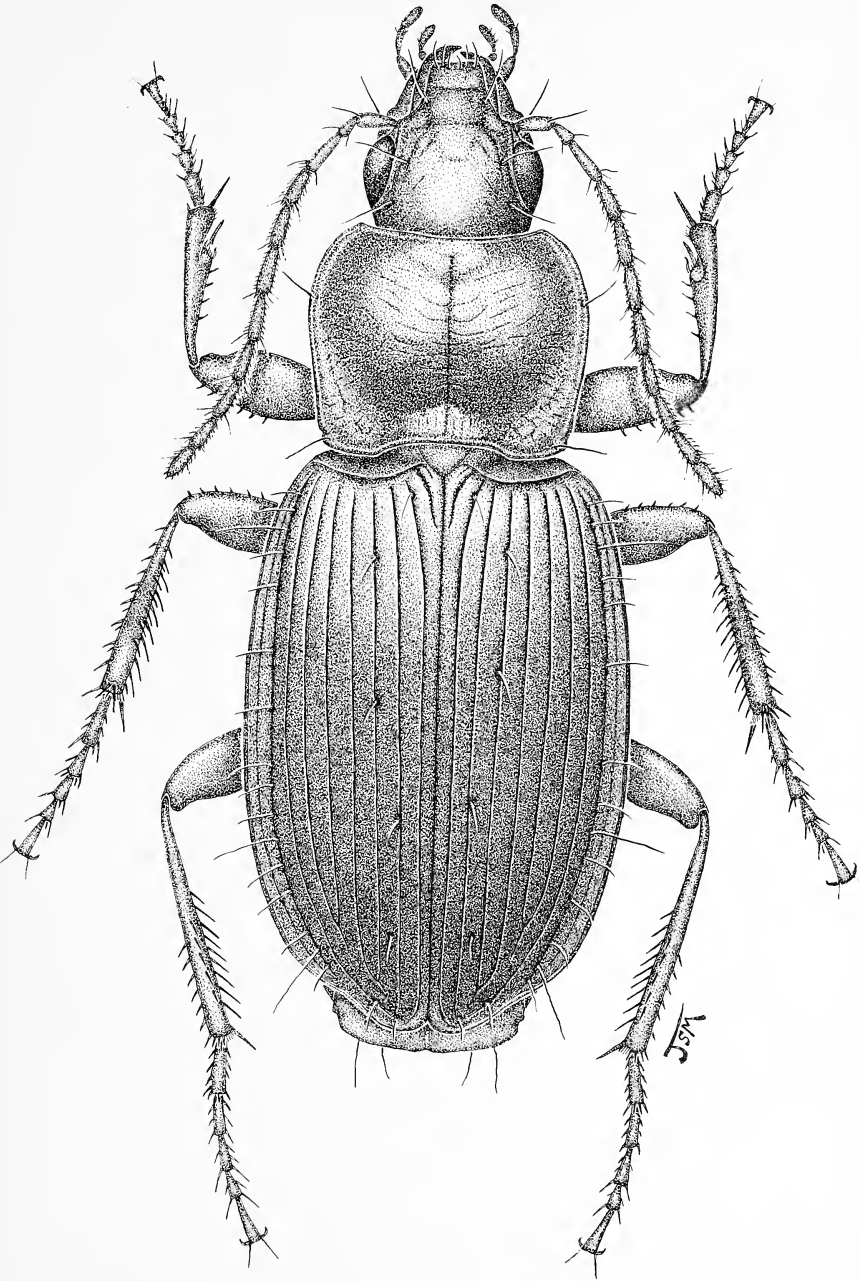
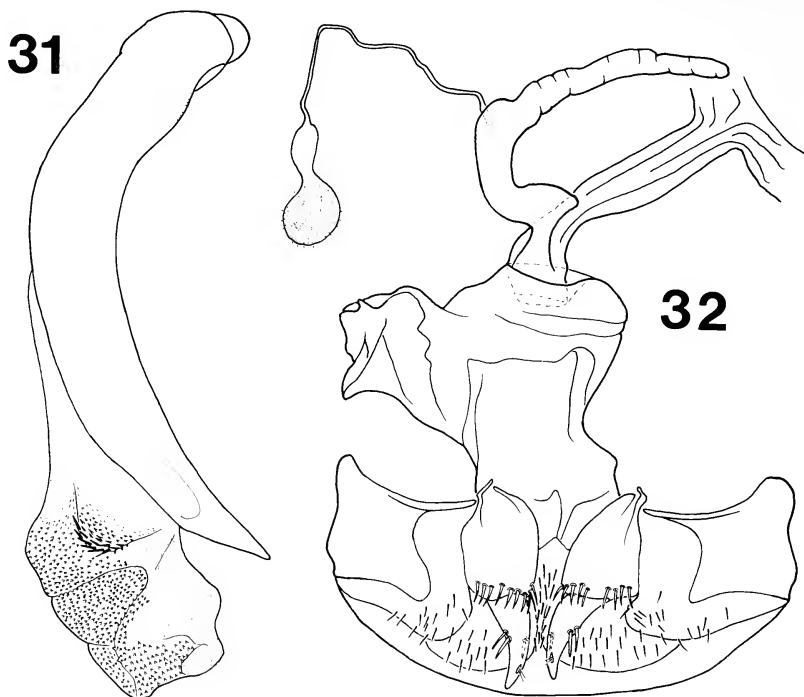


Fig. 30. Female of *T. sulcata*, CA: Shasta Co., Platina.



Figs. 31, 32. *T. sulcata*. 31. Median lobe of aedeagus (lateral view), CA: Trinity Co., Carr Ranger Sta. 32. Female reproductive tract (ventral view), CA: Trinity Co., Fawn Lodge.

*Material examined.* U.S.A.: CA: *Shasta Co.*: Platina (3, CDFA). *Trinity Co.*: Carr Ranger Sta. (3, CAS); Fawn Lodge (3, CAS); Hayfork (2, CAS). *Humboldt Co.*: (6, CAS). *Modoc Co.*: Ft. Bidwell (1, MCZ). OR: no other data (1, MCZ). *Curry Co.*: 10 mi E Brookings (1, CAS). *Coos Co.*: Coos Bay (1, USNM). *Lane Co.*: Eugene (1, USNM). *Benton Co.*: Blodgett (1, MCZ); Corvallis (1, CAS); Mary's Peak, 3,400–3,500' elev. (25, JRLa). *Marion Co.* (1, CAS). WASH.: Wash. Terr. (1, MCZ). W. Wash. (1, MCZ).

#### BIONOMICS AND ECOLOGICAL PREFERENCE

*Tanystoma* possesses a typical Californian distribution (Van Dyke, 1919). The range of *T. maculicolle* nearly encompasses that of the other three species and extends from coastal Baja California del Norte to southern Oregon, west of the Mojave Desert, and in the Sierra Nevada and Cascade mountains. In this area, it is commonly found in open grassland areas, from sea level to 1,600 m elevation. Individuals aggregate in winter, and can be found clustered together under logs and bark of *Eucalyptus* trees growing on open areas. Larval development occurs in winter and early spring (Liebherr, 1984). During June and July, large flights of adults have been reported in the Central Valley of California (Riley, 1882). These flights occur about 2 months after the peak adult eclosion (Liebherr, 1984). Adults are reproductively active only

Table 1. Total numbers of specimens by month for three *Tanystoma* species.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
<i>T. cuyama</i>	13	11	12	3	1	3	0	1	0	2	2	19
<i>T. striata</i> (coast)	4	14	9	3	1	3	0	0	0	8	33	13
<i>T. striata</i> (Sierra)	0	0	1	0	5	8	10	15	6	3	1	1
<i>T. sulcata</i>	0	1	4	7	1	8	0	0	0	6	9	3

during winter and early spring, hence this dispersal occurs in prereproductive adults that will subsequently become quiescent during the driest part of the summer.

*Tanystoma cuyama* is most commonly captured in winter (Table 1), and it occurs in open oak-grassland to chaparral habitats. Adult activity from December to March coincides with winter rains in southern California.

*Tanystoma striata* captures reflect the seasonal conditions in the two portions of its range, the Northern Coastal Ranges and the Sierra Nevada. In the coastal habitats, adults have been taken in largest numbers from October to March (Table 1), with few individuals collected from April to October. In inland habitats on the western slopes of the Sierra Nevada, adults are most abundant from May to September. These complementary periods of abundance indicate that local conditions control the life cycle in this species. It is possible that *T. striata* is active during winter in the Sierra, however, difference in summer activity between coastal and inland habitats is irrefutable.

*T. striata* has been taken repeatedly on San Bruno Mtn., San Mateo Co., in moist grassland habitat. It is absent from drier rocky soil, being restricted to the more mesic slopes at lower elevations. It is found in association with *Omus californicus* Eschscholtz, *Scaphinotus ventricosus* Dejean, *S. cristatus* Harris, *Promecognathus laevis-simus* Dejean, and 3 spp. of *Pterostichus* subgenus *Hypherpes*. In 1981, adults were collected in pitfall traps from January 31 to March 21. Trapping began January 15, and continued until April 15, 1981, but no more *T. striatus* were collected.

*T. sulcata* has been less commonly collected than *T. cuyama* or *T. striata*, with specimens recorded throughout the year (Table 1). It does not appear to be active during the months of July to September, and is more commonly taken in early winter and spring. In Oregon, on Mary's Peak in Benton Co., *T. sulcata* is found in ecotonal habitat between open areas and coniferous forests (J. LaBonte, P. Johnson, pers. comm.). This species is seldom found far into forest habitats, being restricted to open areas at the forest edge or on roadsides. This habitat generally has a dense growth of grasses and *Senecio* sp. Associated carabids include *Trachypachus holmbergi* Mannerheim, *Scaphinotus marginatus* Fischer, *S. angusticollis* Mannerheim, *Zacotus matthewsi* LeConte, *Harpalus cordifer* Notman, and several species of *Pterostichus* (J. LaBonte, pers. comm.).

#### CLADISTIC ANALYSIS

The relationships among the four species of *Tanystoma* can be estimated by cladistic analysis (Hennig, 1966). The use of shared derived states of characters as a means of hierarchically grouping taxa is the necessary first step in gaining an under-

Table 2. Characters, primitive and derived states, and character state distribution for *Tanystoma* species (0 = primitive state; 1 = derived state; — = does not apply).

Character	Primitive	Derived	<i>T. maculicollis</i>	<i>T. cuyama</i>	<i>T. striata</i>	<i>T. sulcata</i>
1) Aedeagal saccal spines	absent	present	0	1	1	1
2) Number of saccal spines	11-20 spines	15-30 spines	—	1	0	0
3) Pronotal base	rounded	expanded	0	0	0	1
4) Flight wings	dimorphic	brachypterous	0	1	1	1
5) Metathorax length*	$1.0 < c/a < 1.2$	$0.94 < c/a < 1.12$	—	0	1	1
6) Body coloration	uniform	lighter margins	1	1	0	0
7) Body maculations	absent	present	1	0	—	—
8) Dorsal elytral setae	3-5	4-6	1	1	0	0

\* See text and Fig. 19 for explanation.

Table 3. Number of spines in saccal spiny patch of aedeagus for three *Tanystoma* species.

Species/population	Individuals/# spines in patch							
	1	2	3	4	5	6	7	$\bar{x}$
<i>T. cuyamae</i> /Lk. Cachuma	30	27	21	20	19	15	15	21
<i>T. striata</i> /Mt. San Bruno	20	18	18	16	15	14	14	16.4
<i>T. sulcata</i> /pooled	19	15	15	14	12	11	11	13.8

standing of how a group has diversified. An hypothesis of relationships is necessary to hypothesize speciation mechanisms, or to compare patterns of diversification in different groups of taxa.

To determine the primitive and derived states of the differential characters of *Tanystoma* species, the states within the group are compared to those of taxa outside the group. *Rhadine* LeConte is assumed the sister group to *Tanystoma* (Liebherr, in press). This hypothesis of relationship is based on shared derived spermathecal configuration, posteriorly expanded laterobasal pronotal margin, and sparse secondary setation of the integument. The autapomorphous increase in pedicel setation within *Tanystoma* (Fig. 16) is the basis for monophyly of this taxon. Other genera placed in the *Rhadine-Tanystoma* lineage of the subtribe Platynina by Liebherr (in press) include *Anchus* LeConte, *Paranchus* Lindroth, and *Atranus* LeConte. Species in these genera and in other platynine genera were used as additional out-groups for determination of the polarity of character states.

Eight characters were found with differing states among the four species analyzed. A listing of characters, primitive and derived states, and rationale for assigning polarity follow, and are summarized in Table 2.

1) Aedeagal internal sac with a ventrolateral patch of spines; absent = primitive, present = derived. Some *Rhadine* spp. possess patches of spines on the aedeagal sac. The *R. perlevis* group possess a broad plate of flattened spines on the sac (Barr, 1983), however the spiny patch differs in position and size from that seen in *T. cuyama*, *T. striata*, and *T. sulcata*. Spiny patches of varied size and position were observed in *Rhadine nivalis* Horn, *R. jejuna* LeConte, and *R. myrmecodes* Horn. The varied location and saccal spination in *Tanystoma* and *Rhadine*, and its general absence in other closely related genera, implies that the spiny patch in *Tanystoma* is uniquely derived. It is apparent that saccal spination is labile within the *Rhadine-Tanystoma* lineage, but it may serve as a gradistic or trend character, indicative of similar genetic bases for aedeagal sac sclerotization.

2) The number of spines in the saccal spiny patch varies between 15 and 30 in *T. cuyama*, 14 and 20 in *T. striata*, and 11 and 19 in *T. sulcata*, based on samples of 7 individuals per species (Table 3). Using the Wilcoxon rank-sum test on spine number, *T. cuyama* has significantly more saccal spines than *T. striata* ( $P < 0.049$ ) and *T. sulcata* ( $P < 0.006$ ). Based on the presence of a spiny patch as derived (Character 1), the higher number of saccal spines seen in *T. cuyama* is assumed a further derived state.

3) The pronota of *Tanystoma* and *Rhadine* adults always possess posteriorly expanded laterobasal margins. This expansion is maximally developed in *T. sulcata*



(Fig. 11). The greatly expanded laterobasal margin, and quadrate pronotal shape of *T. sulcata* is assumed derived.

4) Flight wing development varies among the species of *Tanystoma*. *T. maculicolle* individuals may be either macropterous or brachypterous. *T. cuyama*, *T. striata*, and *T. sulcata* are exclusively brachypterous. Brachyptery is assumed derived.

5) Among the 3 brachypterous species, metathoracic development can be evaluated using the ratio of inner lateral length (c) to transverse width (a) of the metepisternum (Figs. 15, 19). *T. cuyama* possesses a somewhat more elongate metathorax than either *T. striata* or *T. sulcata* (Fig. 19). As metathoracic development is directly correlated with flight wing configuration in *T. maculicolle*, reduction of the metathorax is assumed derived. Based on the Wilcoxon rank-sum test, the distribution of the ratio c/a is significantly different in *T. cuyama* versus *T. striata* ( $P < 0.005$ ), and *T. cuyama* versus *T. sulcata* ( $P < 0.002$ ). Because of this, *T. sulcata* and *T. striata* are considered derived with respect to metathoracic development.

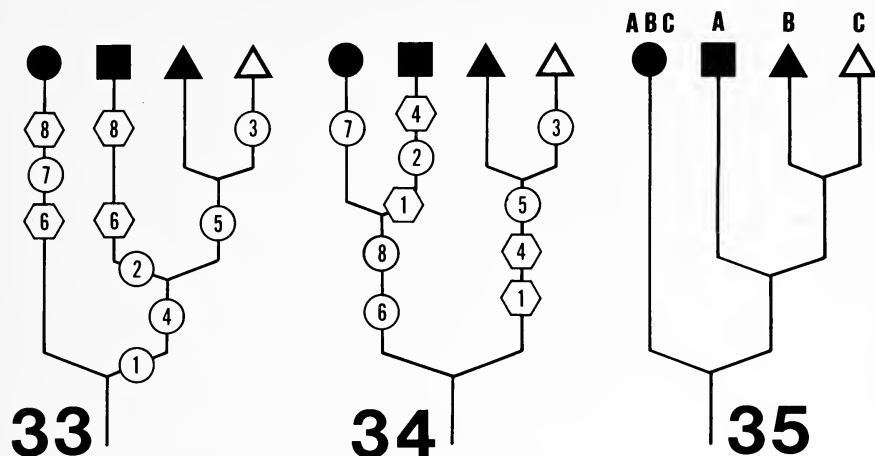
6) Most platynine carabids possess uniform body coloration. Such is the case throughout *Rhadine*. The contrasting testaceous lateral body margins of *T. maculicolle* and *T. cuyama* are considered a derived state of body coloration.

7) *T. maculicolle*, in addition to lighter body margins, possesses distinctly patterned discal maculae on the pronotum and elytra. This patterning is considered a further derived state of body coloration.

8) Presence of 3 dorsal elytral setae is the state most generally distributed throughout the Platynini. With the exception of only a few species, *Rhadine* is comprised of species, the adults of which exhibit 5 or fewer dorsal elytral setae (Barr, 1960, 1965, 1974, 1983; Barr and Lawrence, 1960; Bolivar y Pieltain and Hendrichs, 1964). Specimens of *T. sulcata* and *T. striata* possess 3 to 5 dorsal elytral setae. Specimens of *T. maculicolle* and *T. cuyama* possess 4 to 6 dorsal setae. The increased number of 4–6 setae is assumed derived.

All characters are unit coded, with a single derived state per numbered character. If a character complex is represented by a 2 step character state transformation ( $0 \rightarrow 1 \rightarrow 2$ ), only those taxa coded derived for the first transformation step are included in the coding of the more derived character state. For this data set, 3 pairs of such nested characters are present; 1 and 2, 4 and 5, 6 and 7; and in the coding, taxa coded primitive for the first more inclusive character are deleted from the coding process for the second character (Table 2). When such hierarchical characters are placed on a cladogram, care must be taken so that the most derived state of a multi-state character is placed most distal to the first step of the transformation series.

Based on the distribution of shared derived character states (Table 2), two cladograms are equally parsimonious (Figs. 33, 34). Both cladograms require parallel derivation in 2 characters; character 6 (body color) and 8 (dorsal elytral setae), or character 1 (aedeagal spiny patch) and character 4 (brachyptery). Of these 4 characters, the presence of a spiny patch on the aedeagal sac is perhaps the best indicator of phylogeny. This structure is in the same position on the sac in all 3 species, and is comprised of similar stout spines, giving evidence of its homology. Brachyptery is not a good character upon which to base monophyletic groupings of carabids, as this phenomenon of reduction occurs throughout the family. Body coloration and dorsal elytral setal number are also poor characters for grouping, as both are variable among



Figs. 33–35. Cladograms of *Tanystoma* species (circle = *T. maculicolle*; square = *T. cuyama*; solid triangle = *T. striata*; open triangle = *T. sulcata*). 33. Cladogram with parallelisms in characters 6 and 8 (hexagons). 34. Cladogram with parallelisms in characters 1 and 4. 35. Preferred cladogram showing area-taxon relationships (A = South Coast and Peninsular range mountains; B = North Coast and Sierran ranges; C = Vancouverian portion of North Coast ranges in California and Oregon).

closely related species in many groups. Some carabid species may even be polymorphic for body coloration, with the different color morphs determined by a single allele (Liebherr, 1983). Based on this evaluation of characters, the pectinate cladogram (Fig. 33) is chosen as the hypothesized estimation of species relationships within *Tanystoma*.

#### HISTORICAL BIOGEOGRAPHY

Given the hypothesized phylogenetic relationships (Fig. 33), the geographic distributions of the species of *Tanystoma* can provide insights for cladogenesis in this group. The distribution of *T. maculicolle*, the wing-dimorphic species, nearly encompasses the distributions of the other 3 species (Figs. 25, 27). An analysis of the taxon-area cladogram for the 4 species of *Tanystoma* (Fig. 35) can be done using methods of Platnick and Nelson (1978). Because *T. maculicolle* is found in the sum of areas of the other 3 species, we can make no statement regarding the nature of the vicariance event represented by the basal dichotomy. If we assume allopatric speciation as the mode of diversification, at least 2 acts of dispersal would be needed to account for the pattern of areas and taxa. One scenario would involve *T. maculicolle* inhabiting area BC at the first cladogenetic event, and subsequently dispersing into A, whereas the ancestor of *T. cuyama-striata-sulcata* dispersed from A to B and C before subsequent speciation. Such analysis requires an unjustifiable assumption of a center of origin for *T. maculicolle*.

The 3-taxon statement involving *T. cuyama*, *T. striata*, and *T. sulcata* can be

compared to patterns of diversification in other groups, and to well substantiated geologic events. The geographic distributions of these 3 species conform to those observed in many other groups. The Southern Coast Ranges from Monterey to the Transverse Ranges have long been recognized as an area of mixing of the Vancouverian and Californian faunas (Linsley, 1939, 1958; Van Dyke, 1919, 1926, 1929, 1939). Raven and Axelrod (1978) summarize congruent distributional data for the Madro-Tertiary and Arcto-Tertiary geofloral associations.

Several barriers to dispersal have existed in this area prior to, and during the Pleistocene. The San Joaquin Valley entered the Pacific in the vicinity of the Transverse Ranges up until Plio-Pleistocene times (Peabody and Savage, 1958; Wahrhaftig and Birman, 1965). North of the Southern Coast Range, the Salinas Valley has periodically served as a barrier until the late Pleistocene (Wahrhaftig and Birman, 1965). Monterey is the southern limit of distribution for large numbers of mammal species (Hall, 1981), as well as a number of amphibian and reptile species (Anonymous, 1963 et seq.). Among plants, the Southern Coast Range is the site of a large number of apoe endemic species (Stebbins and Major, 1965). Apoe endemics are allopolyploids exhibiting restricted distribution, which are derived from widespread lower ploidy-level parental species. Their occurrence can show past sympatry of parental species that are now parapatric, or largely allopatric (Grant, 1954a, b; Lewis and Lewis, 1955).

Past separation of the biota in the Coast Range north of San Francisco Bay from that in the mountains farther north in Oregon and northern California is suggested by a more modest number of examples, generally involving infraspecific variation. Differences within *Scaphinotus rugiceps* (Horn), a species distributed from Mendocino Co., California to Lane Co., Oregon, prompted Gidaspow (1968) to recognize two subspecies, with subspecific limits roughly correlated with the Siskiyou River. Infraspecific variation in species of *Nebria* (Coleoptera: Carabidae) includes 3 hypothesized vicariance events between presently isolated sets of population on mountains in northern California versus southern Oregon (Kavanaugh, 1980). In the genus *Coelocnemis* (Coleoptera: Tenebrionidae), specimens of *C. californica* Mann. in the Northern Coast Range near San Francisco Bay do not differ significantly from those in Oregon (Doyen, 1973). In general, divergence among taxa from San Francisco to Oregon is much less pronounced than in the area of the Southern Coast Range. Often, subspecific designations have been used to illustrate the variation observed. Whether this divergence is the result of vicariance, as observed in the isolated montane populations of *Nebria*, or primary diversification of parapatric populations, cannot always be determined.

The terminal 3-taxon statement (Figs. 33, 35) from the analysis of *Tanystoma* is compatible with what is known of geologic events, and the general patterns observed in other groups. Vicariance in the southern portion of the aggregate species ranges can be explained by climatic oscillations due to glacial episodes during the Pleistocene. The sclerophyllous plant communities of California, in place since the Miocene, oscillated dramatically during the Pleistocene in response to changing rainfall patterns, changing seasonality, rapid orogeny, and changing edaphic factors (Axelrod, 1973). I hypothesize that during this time the distributional range of the ancestor of *T. cuyama-striata-sulcata* became fragmented, probably by restriction of grassland

habitat during pluvial periods. Such fragmentation resulted in speciation, with *T. cuyama* arising in the Southern Coast Range, and ancestral *T. striata-sulcata* to the north. The range of the ancestor of *T. striata* and *T. sulcata* was subsequently fragmented. The southern portion of the range of *T. sulcata* corresponds with the distribution of the North Coast floristic province (Stebbins and Major, 1965) and Vancouverian zoogeographic province (Van Dyke, 1919). This area has a high frequency of relictual plant species that are remnants of the Arcto-Tertiary Geoflora (Stebbins and Major, 1955). Vicariance of the ancestral range of *T. striata* and *T. sulcata* can be explained if the grassland-chaparral habitat was fragmented during glacial maxima, with present-day sympatry caused by expansion of grassland and chaparral.

The larger number of speciation events caused by vicariance in or near the Southern Coast Ranges suggests this mechanism has been working since early in the Pliocene-Pleistocene, when orogenic processes were less advanced, and climatic oscillations less severe (Axelrod, 1973). Only during later Pleistocene periods did climatic oscillations become great enough to fragment distributional ranges along the North Coast. In summary, a similar mechanism caused both vicariance events in *Tanystoma*, however the timing of vicariance progressed from south to north.

The known range of *T. cuyama* is comprised of two disjunct areas: the Peninsular Mountain Range northeast of San Diego, and the Southern Coast Range north of Ventura Co. (Fig. 27). This disjunction is seen in a number of plant species (Munz, 1935), and represents the present-day unsuitability of the Los Angeles basin for more mesically adapted species.

The sister group of *Tanystoma* is hypothesized to be the genus *Rhadine* (Liebherr, in press). *Rhadine* is a Sonoran faunal associate, also found in the Great Basin. Its only entry into California is in the Mojave Desert, Owens Valley, and Modoc Plateau where it breaks through to west of the Sierra Nevada-Cascade axis. The sister genera *Omus* and *Amblycheila* of the Cicindelinae exhibit a similar vicariant pattern (Van Dyke, 1926; Cazier, 1942; Vaurie, 1955). As with *Rhadine* and 3 species of *Tanystoma*, *Omus* and *Amblycheila* are comprised of wingless species with endemic distributions. They are also found in the same habitats as *Rhadine* and *Tanystoma*, suggesting that similar vicariant mechanisms may have operated on all these groups.

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NEOTYPE DESIGNATION FOR  
*SCARITES SUBTERRANEUS* FABRICIUS 1775  
(COLEOPTERA: CARABIDAE: SCARITINI)

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*Abstract.*—The presumed type of *Scarites subterraneus* Fabricius 1775 (described from "America") deposited in the Zoological Museum at Copenhagen, Denmark is not conspecific with what is generally regarded as *Scarites subterraneus* F. The Copenhagen specimen compares favorably with both specimens and descriptions of *Scarites abbreviatus* Dejean, a species endemic to the Madeira Islands. There is sufficient doubt regarding the type status of the Copenhagen specimen that a neotype is proposed for *Scarites subterraneus* F. in order to assure taxonomic stability. The origin of the neotype is Pt. Pelee, Ontario, Canada. The species concept adopted equals *Scarites subterraneus* s. str. of Bänninger (1938). The species concept of *Scarites subterraneus* in Lindroth's *The ground-beetles of Canada and Alaska* (1961-1969) includes two species, one of which is *Scarites subterraneus* s. str. of Bänninger. A diagnosis is provided for the concept of *Scarites subterraneus* adopted here.

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As part of a current systematic revision of the West Indian Scaritini (Coleoptera: Carabidae) I find it necessary to stabilize the species concept of *Scarites subterraneus* Fabricius (1775:249), a common North American species which ranges south into Cuba. Stabilization of the species concept is also desirable because *Scarites subterraneus* F. is the type species of the genus, and the nominate subgenus (Bänninger, 1938:114; Lindroth, 1961:128; Basilewsky, 1973:178).

Lindroth (1961:129) noted that the Copenhagen specimen regarded as the type of *Scarites subterraneus* F. (see Zimsem, 1964:41) is not conspecific with what is commonly regarded as *Scarites subterraneus* F. by American authors. I have examined the Copenhagen specimen and I concur with Lindroth's observation. The Copenhagen specimen belongs to the subgenus *Scallophorites* (Bänninger, 1938:153; Reichardt, 1977:388). *Scallophorites* spp. are entirely Old World except for two taxa assigned to the group from South America (Bänninger, 1938). The Copenhagen specimen is definitely an Old World form. Although the specimen is lacking both hind legs, making identification difficult, other anatomical characters compare favorably with both specimens and descriptions (specimens deposited in the United States National Museum) of *Scarites abbreviatus* Dejean (1825:379), a species endemic to the Madeira Islands (Bänninger, 1938:177).

I have also examined two specimens deposited in the Hunterian Collection at Glasgow (see Staig, 1931:25) which presumably may have been examined by Fabricius. These are likewise Old World *Scallophorites*, bearing no locality or identification labels, and representing yet another species of unknown identity. There is no evidence that Fabricius ever saw the Glasgow specimens.

Fabricius (1775:249) gave the type locality of *Scarites subterraneus* as "America." Although the type locality given could be in error, there are several reasons to doubt the type status of the Copenhagen specimen despite the handwritten "subterraneus" label, which may in fact be in Fabricius's hand, and despite the listing of the specimen in Zimsem (1964:41).

Fabricius gives the source of material of *Scarites subterraneus* as "Dom. Lewin," here referring to William Lewin (the elder), one of the early British lepidopterists (Lisney, 1960:286). Fabricius undoubtedly examined Lewin's collection during one of his early visits to England during the years of 1772–1775 (see Hope, 1845:viii).

According to Tuxen (1967:8–9), Fabricius consistently used the designation "Mus." for specimens deposited in other persons collections, while specimens lacking this designation were deposited in Fabricius's own collection (i.e., "Mus Dom. Banks" would translate as "in the collection of Banks"; whereas "Dom. Lewin" would translate as "from Lewin"). Unfortunately, Tuxen's generalization is not true (e.g., *Scarabaeus validus* Fabricius, 1775:6 "Habitat in Brasilia. Dom. Bancks." (sic), type in London; *Scarabaeus laborator* Fabricius, 1775:18 "Habitat in stercore bovino Brasiliae. D. Banks.," type in London; *Scarabaeus meliboes* Fabricius, 1792:20 "Habitat in America boreali Dom. Lee," type in Oxford; *Scarabaeus mopsus* Fabricius, 1792:58 "Habitat in India orientali. Dom. Lee.," type in Oxford) (see Zimsem, 1964). Consequently, there is no real evidence that Lewin's specimen(s) of *Scarites subterraneus* ever left England.

One must also realize that the species concept of Fabricius and his contemporaries corresponded approximately to today's generic concept and that there were no rules regarding type specimens at that time. Fabricius (1775) placed six species within his new genus *Scarites*; all are now in different genera and three are now placed in other families: *Scarites subterraneus* F. (Scaritini: Scaritina); *Laccopterum cyaneum* (F.) (Scaritini: Carenina); *Clivina fossor* (L.) (= *arenarius* F.) (Scaritini: Clivinina); *Oryzaephilus surinamensis* (L.) (= *cursor* F.) (Cucujidae); *Uleiota planata* (L.) (= *arabs* F.) (Cucujidae); and *Orthocerus clavicornis* (L.) (Colydiidae). Fabricius's concept of *Scarites subterraneus* must have been broad since he later (1801:122) reports this species from both America and southern Europe. This must have been a common situation for the time, when identifications relied largely on terse Latin descriptions and memory. The specimen at Copenhagen, if actually seen by Fabricius, could easily be a specimen that he acquired after 1775 and proudly curated by adding a "subterraneus" label. Fabricius did describe several Coleoptera from the Madeira Islands: *Carabus maderae* F., 1775, *Carabus vividus* F., 1801, and *Dytiscus lanio* F., 1775 (Zimsem, 1964).

I have discussed the whereabouts of the Lewin collection with several systematic entomologists at the British Museum (Natural History) (see Acknowledgments) and have consulted Horn and Kahle (1935–1937) and Chalmers-Hunt (1976) without uncovering a shred of information. I have examined a specimen identified as *Scarites subterraneus* in the Banks Collection at the British Museum (Natural History); however, there is no evidence that Fabricius ever saw this specimen.

Considering (1) the Copenhagen specimen can only questionably be regarded as the type of *Scarites subterraneus* Fabricius and (2) the improbability of locating a

specimen attributable both to the Lewin collection and to Fabricius, I elect here to designate a neotype for *Scarites subterraneus*, judging the type to be lost. This decision meets all the provisions for designating neotypes under Article 75 of the International Code of Zoological Nomenclature (Int. Comm. Zool. Nomen., 1964). The Copenhagen specimen has not been previously designated holotype or lectotype in spite of three world revisions of *Scarites*: Chaudoir, 1855; Chaudoir, 1880; and Bänninger, 1938.

The species concept of *Scarites subterraneus* F. adopted here equals *Scarites subterraneus* s. str. of Bänninger (1938). The species concept of *Scarites subterraneus* in Lindroth (1961) includes two species based upon examination of specimens determined by Lindroth at the Canadian National Collection (Ottawa). One of these is *Scarites subterraneus* s. str. of Bänninger; the other is a form whose correct name remains yet to be determined. The latter possesses antennae with antennomeres 8–10 distinctly longer than broad, not as broad as long like *Scarites subterraneus*. The present concept of *Scarites subterraneus* F. appears to trace back as far as Melsheimer (1806).

Lindroth (1961:128) restricted the type locality of *Scarites subterraneus* F. to the north shore of Lake Erie, Ontario. I have selected a male specimen, identified by Lindroth as *Scarites subterraneus* F., as neotype. This specimen is deposited in the Canadian National Collection (Ottawa) and bears the following labels: "Pt. Pelee, Ont 10.VI.1929 L.J. Milne"; "*Scarites subterraneus* F. Det. Lindroth 1958"; "NEO-TYPE *Scarites subterraneus* F. des. S.W.Nichols 1984." The specimen is macropterous. The genitalia have been dissected and placed beneath the specimen in a glycerine-filled microvial. Deposited with the neotype are two female specimens with the same locality label. Both females are also macropterous.

*Scarites subterraneus* F. may be distinguished from all other North American *Scarites* based upon the following diagnosis:

Antennomeres 8–10 as broad as long (moniliform); metasternum behind mesocoxa longer than metacoxa; macropterous; setiferous puncture in basal half of interval 3 of elytron usually present; elytral striae varying from virtually absent (some western *S. subterraneus*) to consisting of well-impressed grooves, but always lacking minute punctulae; hindbody generally between 7.5 to 10.0 mm in length (not including peduncle).

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**ANTHRENUS PIMPINELLAE F., A PALEARCTIC DERMESTID  
ESTABLISHED IN EASTERN NORTH AMERICA  
(COLEOPTERA: DERMESTIDAE)**

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*Abstract.*—*Anthrenus pimpinellae* F., a widespread Palearctic dermestid, is reported from Delaware and Pennsylvania, the first confirmed records of this species for the Western Hemisphere. *Anthrenus lepidus* LeConte and *A. occidentis* Casey, considered junior synonyms of *A. pimpinellae* since the early 1900's, herein are removed from synonymy with *A. pimpinellae*. A table of external morphological characters separating these 3 species is given. The biology and habits of this introduced dermestid are reviewed and summarized from the European literature. A diagnosis and illustration of the adult are provided, along with a new key to the species of *Anthrenus* occurring in North America east of the Mississippi River.

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The genus *Anthrenus* Schaeffer is comprised of 83 species (Mroczkowski, 1968) that occur primarily throughout the Holarctic region, with a number of species also known from the southern hemisphere. In the United States there are at least 13 species placed in 5 subgenera. Seven species are shared with the Palearctic region, presumably accidentally introduced into North America with commerce.

Ever since Arrow (1915) synonymized *Anthrenus lepidus* LeConte and *A. occidentis* Casey with the European *A. pimpinellae* F., entomologists have assumed that the latter is indigenous to the United States. Hinton (1945) accepted the synonymy, as did Mroczkowski (1968), a specialist in the genus *Anthrenus*. In our opinion, however, Arrow erred in synonymizing these forms, and the true *A. pimpinellae* has not been recognized previously from the Western Hemisphere.

*Anthrenus pimpinellae*, a common Palearctic dermestid known from Europe, northern Africa, Asia, and portions of the Oriental region, was recently detected in the New World, based on specimens collected in 1984 by ERH and AGW at Newark, Delaware (New Castle Co.). Three specimens were collected from inflorescences of viburnum (*Viburnum dilatatum* Thunb.) and 1 specimen from inflorescences of *Deutzia lemoinei* Hort. Lemoine ex Bois on the campus of the University of Delaware, on May 28, June 2, and June 6, 1984. In addition, older material of this species was discovered in the collection of the Pennsylvania Department of Agriculture. Two rubbed specimens had the label data: "Jeannette, Pa."/"5300." As the result of a thorough search of an early accession catalog (containing records initiated by H. A. Surface of the PDA in 1904), and examination of an issue of the *Monthly Bulletin* (Surface, 1906), AGW found that these two specimens, with accession number "5300," were among "1600 species and varieties" of Pennsylvania Coleoptera received on

March 22, 1906 from H. G. Klages of the Carnegie Museum (Pittsburgh, Pennsylvania).

In this paper we briefly describe the habits and habitat of *A. pimpinellae* based on the European literature, provide an adult diagnosis and photograph of the dorsal habitus distinguishing this species from *A. lepidus* and *A. occidentis*, and present a key to the species of *Anthrenus* occurring in North America east of the Mississippi River.

*Anthrenus pimpinellae* F.

Within some species of the genus *Anthrenus* there are a remarkable number of variant forms distinguished by arrangements of the colored scales clothing the body, particularly the dorsal surface. *Anthrenus pimpinellae* has been considered such a species; Mroczkowski (1968) lists 2 subspecies and 11 named varieties in addition to the nominate form. The extent to which gene exchange occurs among these various forms has not been demonstrated, however, and whether "*pimpinellae*" consists of one or many species is still a question. Vladimir Kalik of Pardubice, Czechoslovakia, who has been investigating the *A. pimpinellae* complex, believes that there are yet a number of distinct Palearctic species included under the name, some of which are separable by phallic characters only. He considers the nominate form to exist without aberrations, variations or subspecies (*in litt.* to RSB). Should this be true, *A. lepidus* and *A. occidentis* would be excluded from *A. pimpinellae*. Most species of *Anthrenus*, as Mroczkowski recently has shown in his numerous papers, are in fact clearly separable by phallic characters. The male genitalia of *A. lepidus* and *A. occidentis*, however, are apparently identical to those of the nominate form of *A. pimpinellae*. Nevertheless, these two western U.S. forms (whether themselves constituting 1 or more species) possess a suite of characters that appear consistently to separate them from *A. pimpinellae*. Consequently, we herewith remove *A. lepidus* LeConte (1854) and *A. occidentis* Casey (1900) from synonymy with *A. pimpinellae* Fabricius (1775), and cite in the following table the differences separating these species.

*A. pimpinellae*

*A. lepidus*, *A. occidentis*

- |  |  |
|--|--|
| 1. Ratio of width of segment 9 of the male antenna to width of segment 11 nearly 1:1.1.  | Ratio of width of segment 9 of the male antenna to width of segment 11 nearly 1:1.5.                                     |
| 2. Spiracles of abdominal segments 2-5 not enclosed by darkly pigmented lateral extension of tergum, spiracles outside or (usually) at margin of pigmented area. | Spiracles of abdominal segments 2-4, and usually 5, enclosed by pigmented area extending laterad from tergum.            |
| 3. Subbasal band of white scales shorter at suture than at sides of elytron and usually continuous across elytron.   | Subbasal band of white scales, if present, appreciably longer at suture than at sides and not continuous across elytron. |
| 4. Subapical reddish or copper-colored band present on elytron behind subapical white band or patch.   | No distinct subapical reddish or copper-colored band of scales present on elytron behind subapical white band.           |

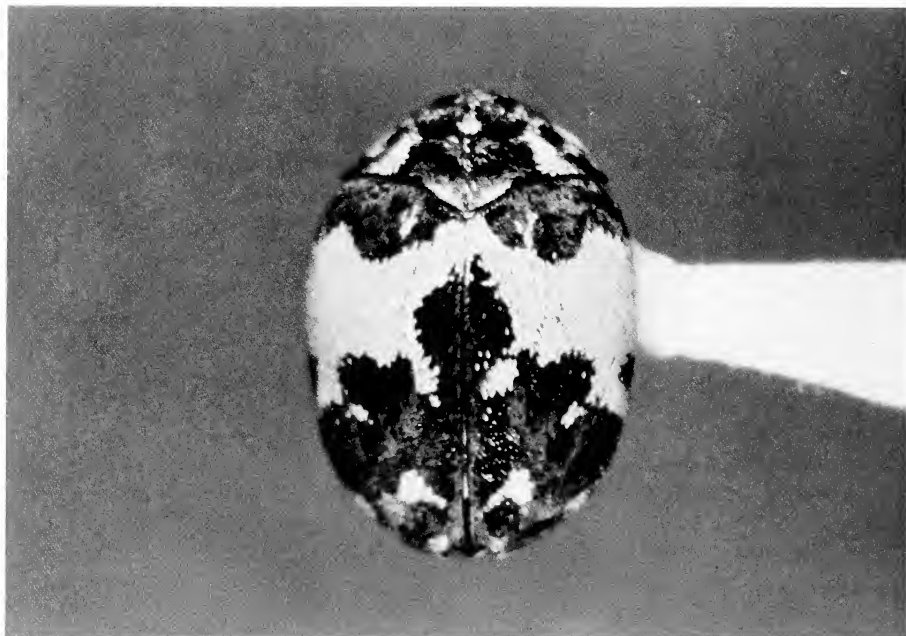
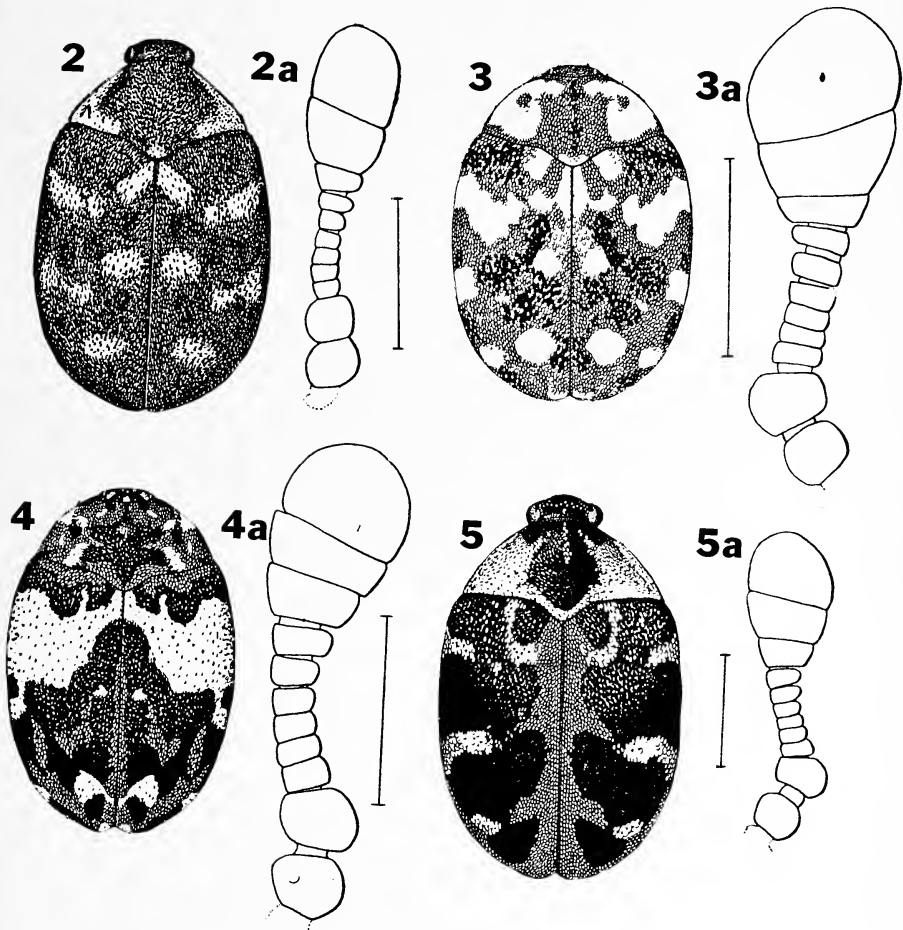


Fig. 1. *Anthrenus pimpinellae* F., typical dorsal habitus.

*Habits and habitat.* This univoltine species (Yokoyama, 1929, reported an occasional 2-year life cycle in Japan) normally overwinters in the adult stage, although larvae that are slow to develop (about 1%) may hibernate. Adults become active in May and are attracted to flowers of various plants. Females deposit 16–48 eggs in spring or early summer, with hatching occurring in 8 days at 26°C and 15 days at 20–22°C; larval development requires 3–4 months. In one experiment larvae took longer to develop on woollen cloth (140–186 days) than on dead insects (96–144 days) or dry fish (86–104 days) (Özer, 1963). Previously, Kunike (1939) noted that larvae prefer wool to dead insects. The pupal stage lasts 8–10 days with pupation taking place in autumn within the last larval skin. In nature, *A. pimpinellae* develops mainly in bird's nests where larvae feed on feathers, hair, dead nestlings, or insect remains. Occasionally it is encountered indoors feeding on wool, stored products, and dried insect specimens, but it is not considered a major household pest. The foregoing biological sketch is based on Hinton's (1945) review, which should be consulted for additional references to *A. pimpinellae* as a pest.

*Recognition.* Adults of *A. pimpinellae* (Fig. 1), when fully scaled, are distinctive. The length is 2.0–3.7 mm. The body is moderately strongly convex and broadly oval with the sides of the elytra distinctly rounded. Scales of the dorsal surface are white, golden, and very dark golden-brown to nearly black; the typical scale pattern is shown in Figures 1 and 4. The pronotum on the middle of each side bears an oval or round patch of dark scales enclosed by paler scales. The elytra have a complete (or nearly complete), broad, transverse patch of white scales on the basal third (as in Figs. 1



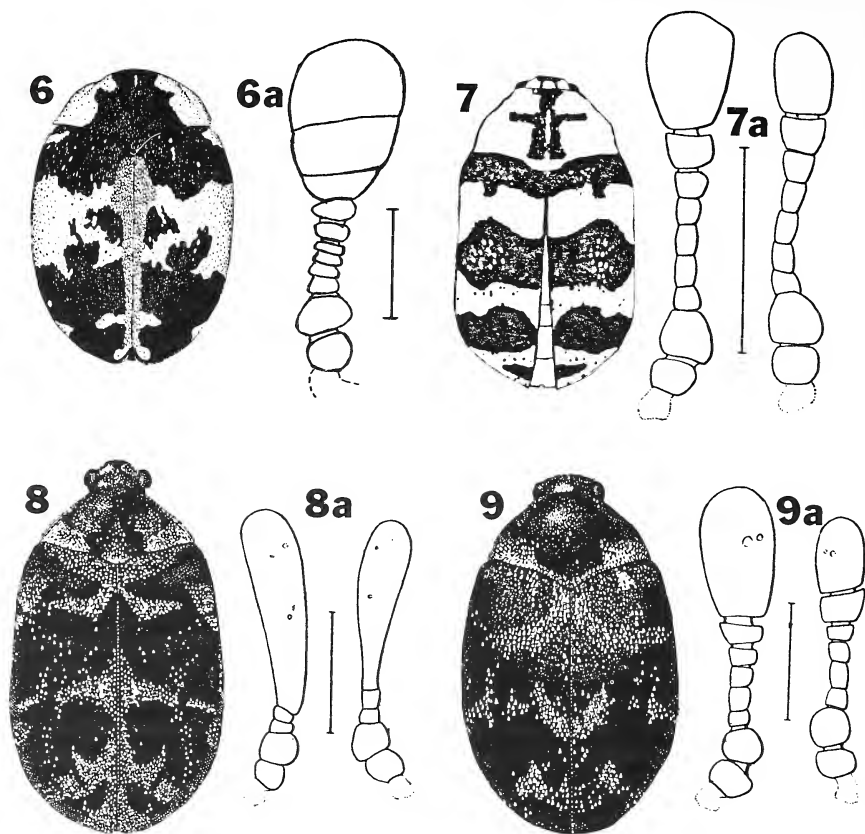
Figs. 2–5. Eastern North American species of *Anthrenus*. 2. *Anthrenus verbasci* (L.); 2a, antenna of same. 3. *A. flavipes* LeConte; 3a, antenna of same. 4. *A. pimpinellae* F.; 4a, antenna of same. 5. *A. scrophulariae* (L.); 5a, antenna of same. All figures reproduced from Hinton (1945). Antennal scale lines = 0.20 mm.

and 4), extending to the suture. Adults of *A. pimpinellae* can be readily separated from other species of *Anthrenus* occurring in eastern North America by the characters given in the following key.

KEY TO NORTH AMERICAN SPECIES OF *Anthrenus* EAST OF THE MISSISSIPPI RIVER

- 1. Antenna 11-segmented with a 3-segmented club (Figs. 2a–6a). Abdomen with discal striae on first sternum ..... 2
- Antenna with 9 or fewer segments; club 1-, 2-, or 3-segmented. Abdomen without discal striae on first sternum ..... 6





Figs. 6–9. Eastern North American species of *Anthrenus*. 6. *Anthrenus thoracicus* Melsh-eimer; 6a, antenna of same. 7. *A. coloratus* Reitter; 7a, male (left) and female (right) antenna of same. 8. *A. fuscus* Olivier; 8a, male (left) and female (right) antenna of same. 9. *A. museorum* (L.); 9a, male (left) and female (right) antenna of same. Figure 6 reproduced from Beal (1983); Figure 7 from Kingsolver (1969); and Figures 7a, 8, 8a, 9, and 9a from Hinton (1945). Antennal scale lines = 0.20 mm.

2. Eye with inner margin entire (subg. *Nathrenus*); typical dorsal habitus as in Figure 2 ..... *A. verbasci* (L.)
- Eye with inner margin interrupted in front of middle by a small emargination (subg. *Anthrenus* s. str.) ..... 3
3. Pronotum with dorsal rim of antennal cavity not or only very slightly dilated; visible abdominal sternum 5 not divided by broad band of black or dark brownish black scales, but sometimes with narrow median line or irregular triangular patch of golden or medium golden brown scales at middle; scales of elytra ovate to obovate, more or less evenly rounded posteriad, with ratio of width to length about 3:5; typical dorsal habitus as in Figure 3, but often with mostly white and golden scales and rarely with nearly all white scales ..... *A. flavipes* LeConte
- Pronotum with dorsal rim of antennal cavity moderately strongly to strongly dilated;



- visible abdominal sternum 5 divided by broad band of black or dark brownish black scales, but sometimes with row of pale scales along anterior margin of sternum; most scales of elytra somewhat parallel-sided and subtruncate posteriad with ratio of width to length mostly 2:5 or narrower; dorsal color pattern various ..... 4
4. Segment 1 of antennal club with length subequal to or longer than length of segment 2; basal  $\frac{3}{4}$  of each side of pronotum with patch of pale scales enclosing a small, oval patch of dark brown to black scales; typical dorsal habitus as in Figure 4 ..... *A. pimpinellae* F.
- Segment 1 of antennal club distinctly shorter than segment 2; basal  $\frac{3}{4}$  of each side of pronotum with patch of pale scales not enclosing darker patch of scales ..... 5
5. Each elytron with 3 more or less equally spaced, transversely undulate patches of white scales meeting or nearly meeting dilations of reddish sutural stripe; typical dorsal habitus as in Figure 5 ..... *A. scrophulariae* (L.)
- Each elytron with subbasal and submedian transverse bands expanded and coalescing laterally to form a large lateral white patch; typical dorsal habitus as in Figure 6 .... *A. thoracicus* Melsheimer
6. Antenna 9-segmented; club 3-segmented (Fig. 7a) (subg. *Anthrenops*); typical dorsal habitus as in Figure 7 ..... *A. coloratus* Reitter<sup>1</sup>
- Antenna 5-, or 8-segmented; club 1-, or 2-segmented ..... 7
7. Antenna 5-segmented; club 1-segmented (Fig. 8a) (subg. *Helocerus*); typical dorsal habitus as in Figure 8 ..... *A. fuscus* Olivier<sup>1</sup>
- Antenna 8-segmented; club 2-segmented (Fig. 9a) (subg. *Florilinus*) ..... 8
8. Males: Antenna with segment 8 at least 5 times longer than segment 7 (Fig. 9a). Females: Ratio of length of segment 7 to segment 8 from 1:2.8 to 1:2.1 (Fig. 9a); typical dorsal habitus as in Figure 9 ..... *A. museorum* (L.)
- Males: Antenna with segment 8 only 2.8 to 2.1 times longer<sup>2</sup> than segment 7. Females: Ratio of length of segment 7 to segment 8 from 1:2.2 to 1:1.4; typical dorsal habitus similar to *A. museorum* ..... *A. castaneae* Melsheimer

The only remaining species of *Anthrenus* recorded in eastern North America is *A. caseyi* Dalla Torre, described from New York. RSB suspects that *A. caseyi* is conspecific with *A. castaneae*, but this needs to be verified by examination of the type of *A. caseyi*.

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<sup>1</sup> Both *A. coloratus* (Kingsolver, 1969) and *A. fuscus* (Mertins, 1982) have only recently been recognized as occurring in the United States.

<sup>2</sup> The ratios in females of *A. museorum* overlap the ratios in males of *A. castaneae*. There is, however, in *A. museorum* a noticeably longer antennal cavity, so that females of the species are easily separated from males of *A. castaneae*.

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## NEW HOST ASSOCIATIONS FOR CERAMBYCIDAE (COLEOPTERA) FROM SELECTED SPECIES OF LEGUMINOSAE AND RUTACEAE

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*Abstract.*—Twenty-four new cerambycid host associations are reported from southeastern Texas. Specimens were reared from *Cercis canadensis*, *Sesbania drummondii*, *Sophora secundiflora*, *Zanthoxylum clava-herculis*, and *Zanthoxylum fagara*. *Plectromerus dentipes* is recorded for the first time from Texas.

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The Cerambycidae of Texas have been intensively studied during the past decade (see Hovore and Giesbert, 1976; Hovore et al., 1978; Turnbow and Wappes, 1978, 1981; Hovore and Penrose, 1982; and Rice et al., 1985). Data from these observations have focused primarily on larval and adult host associations and geographical distributions.

This study reports 24 new larval cerambycid host associations from southeastern Texas and one new state record. Three species of Leguminosae; *Cercis canadensis* L., *Sesbania drummondii* (Rydb.) Cory, and *Sophora secundiflora* (Ort.) Lag. ex DC. and two species of Rutaceae; *Zanthoxylum clava-herculis* L. and *Zanthoxylum fagara* (L.) Sarg. were specifically selected for this study. No cerambycids have been reported from *S. drummondii* or *S. secundiflora*. *Zanthoxylum* was selected because of the numerous beetle species that are known to use it as a host, including the recently described *Nathriobrium methioides* Hovore.

Many cerambycid species are opportunistic, with ovipositing females attracted to injured, dying, or dead woody perennials. After the eggs are laid in a plant, the xylophagous larvae usually are restricted to the internal cortex and/or subcortical layers of the host. This aspect of cerambycid biology permits the infested hosts to be collected and stored in individual rearing containers, so the adult beetles can be collected as they emerge. Specific larval host associations for the emerging species then can be determined. Listed below are host plants, the associated cerambycids, the date(s) of emergence, and the location where the host was collected. Insect specimens are in the collection of the author.

### *Cercis canadensis*

*Plectromerus dentipes* Olivier from Wharton Co., Wharton, 7/22-VI-84. Six specimens emerged from this host and represent a new state record. The species has previously been reported from Florida to Louisiana (Linsley, 1963).

*Obrium maculatum* (Olivier) from Wharton Co., Wharton, 7-VI-84.

*Ecyrus arcuatus* Gahan from Wharton Co., Wharton, 17-IV-84.

*Sesbania drummondii*

*Obrium maculatum* (Olivier) from Aransas Co., Aransas Nat'l. Wildlife Refuge, 7-IV-84 through 17-V-84 and Matagorda Co., 2 mi SE Blessing, 12-IV-84 through 3-V-84.

*Eburia mutica* LeConte from Matagorda Co., 2 mi SE Blessing, 7-VIII-84.

*Anelaphus inermis* (Newman) from Matagorda Co., 5 mi N Markham, V-83 and Wharton Co., 1 mi NW Wharton, 3-V-84.

*Elaphidion mucronatum* (Say) from Matagorda Co., 2 mi SE Blessing, 19-IV-84 through 31-V-84.

*Dendrobias mandibularis* Serville from Matagorda Co., 2 mi SE Blessing, 4-XI-83.

*Aegomorphus modestus* (Gyllenhal) from Matagorda Co., Clemville, 15/17-V-84.

*Ecyrus arcuatus* Gahan from Matagorda Co., 2 mi SE Blessing, 19-IV-84 through 29-VI-84.

*Sternidius mimeticus* (Casey) from Matagorda Co., 2 mi SE Blessing, 4-XI-83.

*Sternidius texanus* (Casey) from Aransas Co., Aransas Nat'l. Wildlife Refuge, 7-IV-84 through 17-V-84 and Matagorda Co., 2 mi SE Blessing, 12-IV-84 through 3-V-84.

*Styloleptus b. biustus* (LeConte) from Matagorda Co., 2 mi SE Blessing, 4-XI-83 and 19-IV-84.

*Leptostylus transversus dietrichi* Dillon from Matagorda Co., 2 mi SE Blessing, 7-VIII-84 through 15-XI-84.

*Sophora secundiflora*

All specimens reared from this host were collected from Calhoun Co., 1.8 mi E Point Comfort along a roadside.

*Eburia mutica* LeConte, 7-V-84 through 29-VI-84.

*Anelaphus m. moestus* LeConte, 29-VI-84.

*Neoclytus a. acuminatus* (Fabricius), 7-IV-84.

*Ataxia crypta* (Say), 17-V-84.

*Sternidius texanus* (Casey), 29-IV-84.

*Zanthoxylum clava-herculis*

*Eburia mutica* LeConte from Wharton Co., 1.7 mi N Wharton along Peach Creek, 3-IX-84.

*Rhopalophora rugicollis* (LeConte) from Wharton Co., 1.7 mi N Wharton along Peach Creek, 20/29-IV-84.

*Sternidius texanus* (Casey) from Jackson Co., 7 mi S Ganado, 12/30-V-84.

*Zanthoxylum fagara*

*Eupogonius pauper* LeConte from San Patricio Co., Lake Corpus Christi State Park, 22-VI-84 through 3-IX-84.

*Leptostylus transversus dietrichi* Dillon from San Patricio Co., Lake Corpus Christi State Park, 14-VIII-84 through 2-XI-84.

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## NEW *OMMATIUS* WIEDEMANN (DIPTERA: ASILIDAE) FROM CUBA AND THE BAHAMAS

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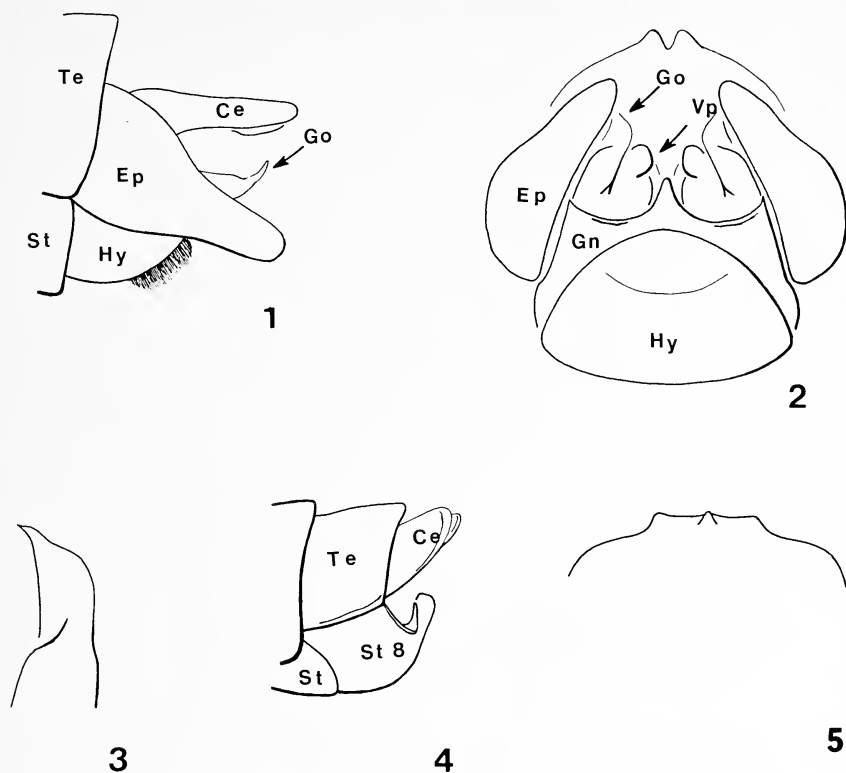
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**Abstract.**—Five new species of *Ommatius* Wiedemann are reported from Cuba and the Bahamas. *Ommatius cubanus*, *O. piliferous*, *O. hispidus* and *O. bipartitus* are from Cuba, and *O. membranous* is from Rum Cay Island in the Bahamas. This report increases the number of species to eight in this region of the Caribbean. The new species are described and their genitalia and the hindleg of the male of *O. hispidus* are illustrated. A key to the species from Cuba and the Bahamas is included. *Ommatius marginellus* (Fabricius) is removed from the list of species from Cuba.

The present paper is the outcome of a study of the *Ommatius* Wiedemann fauna from Cuba and the Bahamas. To date only *O. marginellus* (Fabricius), *O. abana* Curran (1953) and *O. hanebrinki* Scarbrough and Rutkauskas (1983) have been reported from this region of the Caribbean. Bromley (1929) reported that the Cuban *O. marginellus* had the middle and hindtarsi brown and that the scutellum had two marginal bristles. The male type of *O. marginellus* has the basal segment of the midtarsus yellowish and the scutellum lacks marginal bristles. Thus the presence of *O. marginellus* in this region is doubtful (Scarbrough, 1984b). This study reports five new species from Cuba and the Bahamas, with a key to the species.

### KEY TO THE KNOWN SPECIES OF *Ommatius* FROM CUBA AND THE BAHAMAS

- |  |                                    |
|--|------------------------------------|
| 1. Hindtarsus wholly brown or black .....  | 2                                  |
| – Hindtarsus mostly yellowish to reddish yellow .....  | 4                                  |
| 2. Antennal stylus with only 4 rays near the tip .....   | <i>O. abana</i> Curran             |
| – Antennal stylus with numerous rays on most of its length .....   | 3                                  |
| 3. Face with pale yellow pollen and several brown bristles; hindfemur with mostly brown bristles below; male with epandrium and hypandrium rounded apically (Figs. 1, 2); apical 1/3 of hypandrium, with dense pad of long, yellowish pile (Fig. 1) .....                | <i>O. piliferous</i> , new species |
| – Face with bright brassy yellow pollen and only orangish and yellow bristles; hindfemur with pale yellowish or amber colored bristles below; male with epandrium and hypandrium truncate apically (Figs. 10, 11); hypandrium with only fine, short, pile apically ..... | <i>O. bipartitus</i> , new species |
| 4. Anterior surface of forefemur dark basally only .....   | 5                                  |
| – Anterior surface of forefemur wholly dark or dark apically only .....  | 6                                  |
| 5. Hindfemur with 2 preapical dorsal bristles; apical segments of abdomen with numerous unusually strong black bristles (Figs. 19, 20); male with a strong hindtibial spine (Fig. 15) .....  | <i>O. hispidus</i> , new species   |
| – Hindfemur with 1 preapical dorsal bristle; sternite 8 of female with a few thick bristles .....  |                                    |



Figs. 1-5. *Ommatius pilosus*, genitalia: 1-3 male; 4, 5 female. 1. Lateral view. 2. Ventral view. 3. Gonostylus. 4. Lateral view. 5. Sternite 8. Abbreviations: Ce = cercus, Ep = epandrium, Hy = hypandrium, Go = gonostylus, Gn = gonocoxite, Vp = ventral process of gonocoxite, Te = tergite, St = sternite.

- at most; apical abdominal bristles not unusually strong and hindtibial spine absent in males ..... *O. hanebrinki* Scarbrough and Rutkauskas
6. Femora entirely black except base narrowly reddish to reddish yellow; 4 pairs of black strongly proclinate postocular bristles;  $R_{4+5}$  branched at or beyond base of 1st medial cell; 8-10 black ocellar hairs ..... *O. cubanus*, new species
- Forefemur at most with anterior surface entirely brown; postocular bristles short, not strongly proclinate;  $R_{4+5}$  branched well before base of 1st medial cell; 2 ocellar hairs only ..... *O. membranousus*, new species

### ***Ommatius piliferous*, new species**

Figs. 1-5

**Diagnosis.** *Ommatius piliferous* is recognized by 2 weak brownish scutellar bristly hairs, hindtarsus wholly brown, 6 brownish facial bristles, 3rd antennal segment length about twice its width, hindfemur with mostly brown bristles below; female with apical margin of sternite 8 broadly produced; male with the postapical bristle

of midfemur absent, costal margin very slightly produced, apical margin of epandrium rounded, gonostylus strongly flattered dorsoventrally, and a hypandrium with a brushlike pad of yellowish pile on the apical  $\frac{1}{3}$ .

This species is similar to *O. bipartitus*, n. sp. but is easily separated from that species by the pale yellow pollen and 6 brown bristles on the face, and most of the ventral bristles on the hindfemur are black. In contrast, *O. bipartitus* has brassy yellow pollen and orangish to yellow bristles on the face, and the ventral bristles on the hindfemur are almost invariably yellowish or amber colored. The genitalia of both species differ markedly.

*Description.* MALE: Length 12.0 mm. Face and front narrow, pale yellow pollinose, occiput grayish with only a slight tint of yellow above. Antennal, 2 ocellar, 5–6 pairs of postocular and 6 facial bristles brown, palpal and remaining facial vestiture pale yellow to whitish. Occipital pile white; 1–2 pairs of postocular bristles moderately proclinate. Style length  $1\frac{1}{2}$  times the 3 basal antennal segments combined, length of 3rd segment twice its width.

Scutum blackish with mostly brown pollen, brassy yellow behind humeral callus; scutum otherwise and most of scutellum yellowish gray; postalar callus and base of scutellum slightly reddish brown. Scutal bristles black, 2 notopleurals, 1 supra-alar, 1 postalar, 3 strong dorsocentrals posteriorly and scattered pale pile laterally. Scutellum with 2 weak, brownish, bristly marginal hairs, scattered pale pile dorsally. Pleuron mostly gray pollinose with upper half of anepisternum yellowish gray, bristles and scattered pile whitish. Halter reddish brown.

Wing hyaline, with the costal margin thickened and produced very slightly, cells behind slightly yellowish. R-m crossvein before middle of discal cell, 1st medial cell constricted by  $\frac{1}{3}$  beyond middle,  $R_{4+5}$  vein forked at or slightly beyond base of 1st medial cell.

Coxae blackish with gray pollen, bristles whitish. Leg segments mostly yellow to reddish yellow with fore- and midtibiae lightest, brown as follows: apical  $\frac{1}{2}$  of fore- and midfemora and anterior surface of mid-tibia, apical two-thirds of hindfemur, a narrow apical band on midtibia. Basal tarsomere of fore- and midtarsi yellow except a narrow apical brown band, remaining segments of tarsi dark brown. Most setae and hairs yellowish except dorsally and in dark areas of femora. Bristles of foretibiae, all but 1 or 2 on midtibia, 4 on foretarsus and those below fore- and midfemora long and yellowish. Midfemur with 2 black bristles on anterior  $\frac{1}{2}$  and 2 in anteroventral row; usual postapical bristle absent. Hindfemur with 4 black bristles and 1 yellowish (the latter on basal  $\frac{1}{2}$ ) in posteroventral row; 4–5 blackish bristles in anteroventral row and 2 on anterior surface of brown area of femur, the remaining amber colored with 3–5 on basal  $\frac{1}{2}$  in anteroventral row and 1 basally on anterior surface.

Abdomen blackish with brown pollen, pale brown laterally and ventrally. Pile and weaker bristles mostly whitish, setae dark brown dorsally, beginning with tergite 2, becoming increasingly abundant and longer on apical tergites.

Genitalia (Figs. 1, 2) dark brown to blackish, pile and hair mostly pale yellow. Epandrium with black hairs basally, length about  $1\frac{1}{2}$  times basal width, basal  $\frac{1}{2}$  slightly swollen, apical  $\frac{1}{2}$  tapered, apex rounded. Hypandrium apically rounded, the apical  $\frac{1}{3}$  with a dense, brushlike, pad of pale yellowish pile. Gonocoxite with a deep lateral cup, the inner margin forming a vertical, subovate, plate. Gonostylus (Fig. 3)

flattened dorsoventrally on apical  $\frac{1}{2}$ , margins tapered differentially to form an acute point.

**FEMALE:** Similar to the male with the following differences: length 11.0 mm, palps with 2–3 stiff bristly brown hairs; hindfemur with apical three-fourths brown; hindtibia brown on most of anterior surface, dark brown on apical  $\frac{1}{2}$  to two-thirds completely. Hindfemur with 7 black bristles in anteroventral row; posteroventral row with 4–5 black bristles on apical two-thirds, 2 very long bristly hairs basally. Scutellar bristles much stronger than those of males. Abdomen black with dorsal setae pale amber to yellowish. Tergite 9 (Fig. 4) not noticeably produced posteriorly. Sternite 8 black with scattered, long, black bristles basally, anterior margin broadly produced medially (Figs. 4, 5), with a low ridge, the latter projecting slightly in lateral view. Wing typical of females.

**Holotype** ♂ and **allotype** ♀. Cuba, Gunot (?), #252, Loew collection. Paratypes ♂ Coast below Pico Turquino, June 26–30, 1936, Darlington collection; ♀ San Jose Mts., Santa Clara, Cuba, Aug. 27, 1930, Richard Dow. The holotype and allotype are in the MCZ and the paratypes in the AMNH.

**Variation.** The paratypes differ as follows: the male has only 1 postocular bristle black, the remaining are white. The hindtibiae and all femora are brown on the apical  $\frac{1}{3}$ , the foretarsus has 4 yellowish bristles, and the abdomen is slightly lighter brown on the apical 3–4 segments, rather than black. The female paratype is slightly smaller (10.0 mm), the apical  $\frac{1}{2}$  of the hindfemur is brown and the leg bases are brighter yellow.

**Etymology.** The name *piliferous* refers to the dense brushlike pad of pile on the apical  $\frac{1}{3}$  of the hypandrium.

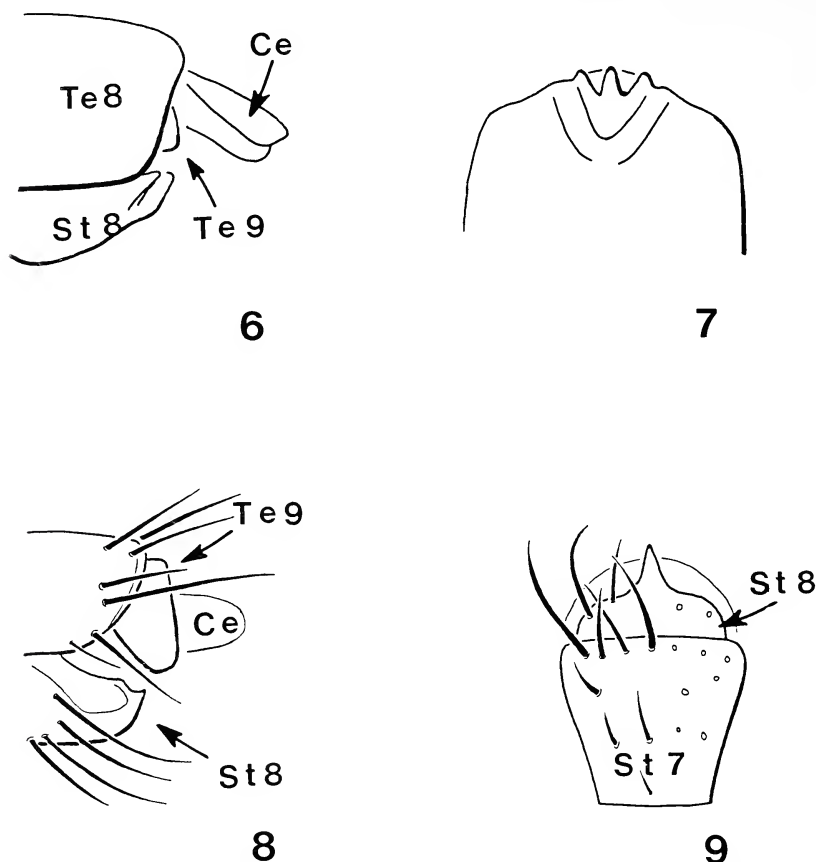
### ***Ommatius cubansus*, new species**

Figs. 6, 7

**Diagnosis.** *Ommatius cubanus* is recognized by a short antennal style, the length slightly more than the 3 antennal segments combined; frontal and 7 facial hairs black, 8–10 black ocellar hairs; 4 pairs of black postocular bristles strongly proclinate; scutellum with 2–3 black bristly marginal hairs; femora mostly shiny black with basal  $\frac{1}{5}$  or less reddish or reddish yellow; basal segments of tarsi mostly yellowish to reddish yellow; bristles of hindfemur almost entirely whitish; abdomen apically narrowed and sternite 8 with a moderately produced apical triangular mound.

*Ommatius cubanus* is similar to *O. vitreus* Bigot (Scarbrough, 1984a) but is easily separated from that species by the strong proclinate postocular bristles, bases of femora narrowly reddish to reddish yellow, and the reddish yellow basal segment of the hindtarsus.

**Description.** **FEMALE:** Length 10.0 mm. Body black. Head grayish to whitish pollinose. Ocellar, 12 pairs of postoculars, frontal, antennal, 7–8 facial bristles black; remaining vestiture of head whitish or white. Ocellus with 2 strong bristles and 7–8 thinner, shorter, black hairs; inner 4 pairs of postoculars strongly curved forward for  $\frac{1}{2}$  or more of their lengths. Antennal style, thick, only slightly longer than 3 basal segments combined, and with only 9 rays below; 3rd antennal length about  $1\frac{1}{2}$  its width.



Figs. 6-9. Female genitalia: 6, 7. *Ommatius cubanus*. 6. Lateral view. 7. Sternites 7-8. 8, 9. *Ommatius membranosus*. 8. Lateral view. 9. Sternites 7-8.

Scutum with mostly brown pollen, brownish yellow behind humeral callus, grayish on sides, scutellum and pleuron. Scutal bristles black; 2 notopleurals, 1 supra-alar, 1 postalar and 4 strong dorsocentrals posteriorly; abundant weak brown hairs on scutum, longer and stronger on sides and between dorsocentrals posteriorly. Scutellum with 3 black marginal bristly hairs; abundant scattered, shorter, whitish and black pile dorsally. Pleuron with scattered, long, whitish pile, abundant on an- and katepisternum and anepimeron, bristles whitish. Halter brownish yellow.

Wing hyaline, subcostal cell brownish, r-m at outer  $\frac{1}{3}$  of discal cell, 1st medial cell not noticeably constricted,  $R_{4+5}$  forked slightly beyond base of 1st medial cell.

Coxae black with gray pollen and white bristles. Leg segments black as follows: all femora except basal  $\frac{1}{4}$  or less, apical  $\frac{1}{4}$  or less of fore- and midtibiae, apices of basal segments (plus entire apical 4 segments) of all tarsi, and apical  $\frac{1}{2}$  of hindtibia; remaining areas yellowish to reddish yellow, with the fore- and midtibiae lightest. Prominent bristles of femora long, whitish; 1 black on forefemur anterobasally, 4



anteriorly and 1 postapical black on midfemur. Hindfemur with 1 very long whitish bristle basally and 1 shorter black apically, 1 black apically and 5 longer whitish bristles in anteroventral row, none at basal  $\frac{1}{4}$ ; 9 longer whitish bristly hairs in posteroventral row of which 7 are on basal  $\frac{1}{2}$ . Fore- and midtibiae with 2–3 whitish bristles including those at apices, remaining bristles of all tibiae and tarsi black.

Abdomen black, tapered narrowly apically, with whitish pile and hairs basally, dorsal setae black becoming increasing more abundant posteriorly, longer in apical corners and along apical margin of tergites. Tergite 9 (Fig. 6) not noticeably projecting posteriorly. Cercus blackish with numerous short black hairs dorsally. Sternites 7–8 (Fig. 7) with several scattered black bristly hairs, median apical surface of sternite 8 with a strongly produced triangular mound (yellowish red), terminating apically as a ridge that traverses the apical margin.

Male unknown.

*Holotype* ♀. Cuba, Buenos Aires, 17–23 June 1939, C. T. Parsons. The holotype is in the MCZ.

*Etymology*. The name *cubanus* refers to the type locality of the species.

### ***Ommatius membranosus*, new species**

Figs. 8, 9

*Diagnosis*. *Ommatius membranosus* is a small species easily recognized by the pale yellowish to whitish facial bristles; 2 weak brownish marginal scutellar hairs; antennal style about twice the length of the 3 segments combined; entire anterior surface of forefemur and most of that of mid- and hindfemora brown; bases of femora, tibiae and most of basal segment of all tarsi yellow; ventral bristles of hindfemur whitish,  $R_{4+5}$  forked before base of 1st medial cell; sternite 7–8 with a few strong black bristles; apical margin of sternite 8 membranous laterally, with a strong ridge medially.

*Ommatius membranosus* is somewhat similar to females of *O. hanebrinki* (Scarborough and Rutkauskas, 1983) and *O. cubanus* in that they are small flies and the hindtarsus in each species is somewhat yellowish. *O. membranosus* differs in that the facial hairs are pale yellow or whitish whereas a few hairs are dark on the upper half of the face of the latter 2 species. In addition, *O. cubanus* has 4 strongly proclinate postocular bristles and the femora are mostly black. These characters are absent in *O. membranosus*. The female of *O. hanebrinki* has the apical and basal ends of the forefemur black, the bases of the leg segments brownish yellow,  $R_{4+5}$  forks at the base of the 1st medial cell and the scutellum lacks marginal bristles. In *O. membranosus*, the anterior surface is uniformly brown, the bases of the leg segments are yellow,  $R_{4+5}$  forks before the base of the 1st medial cell and the scutellum has weak marginal hairs.

*Description*. **FEMALE**: Length 12.0 mm. Body brownish. Face and occiput grayish with a slight tint of yellow. Facial and palpal hairs pale yellow to whitish, beard whitish; 3–4 postoculars, 2 strong ocellar, frontal and all antennal hairs black. Most postocular bristles whitish, none strongly proclinate. Style almost twice the length of the 3 basal antennal segments combined, 3rd antennal segment about  $1\frac{1}{2}$  times width.

Thorax brown dorsally, pleuron slightly reddish brown; scutum mostly brownish pollinose, grayish elsewhere including scutellum and pleuron. Scutal bristles black,

2 notopleurals, 1 supra-alar, 1 postalar and 2 pairs of dorsocentrals posteriorly; scattered, fine, brownish hairs laterally. Scutellum with whitish pile dorsally and 2 fine, brownish, marginal hairs. Pleuron pile and bristles whitish. Halter yellowish.

Wing hyaline, stigma pale brownish, r-m crossvein at or slightly beyond middle of discal cell,  $R_{4+5}$  forked before base of 1st medial cell, 1st medial cell constricted by  $\frac{1}{4}$  beyond middle.

Coxae slightly reddish brown, pollen grayish, bristles whitish. Legs primarily yellow, brown as follows: entire anterior surface of forefemur, apical two-thirds of anterior surface of midfemur, apical three-fourths of hindfemur, apical  $\frac{1}{2}$  or more of anterior surface of hindtibia, apical  $\frac{1}{3}$  of midtibia and narrow apices of foretibia. Apical 4 segments and extreme apices of basal segments of all tarsi brown, basal segments of tarsi mostly yellow. Bristles and hairs of femora and foretibia (excluding apices) yellowish; midfemur with but 2 black bristles on anterior surface, postapical bristle pale yellow. Hindfemur with all bristles whitish, 3 on anterior surface, 4–5 noticeably long bristles in anterior row, none on basal  $\frac{1}{4}$ , 8–10 slightly longer, weaker, bristles in posterior row. Bristles of tarsi and mid- and hindtibiae mostly black, 1 yellowish on foretarsus and hindtibia, 2–3 on midtibia.

Abdomen with hairs and pile whitish on sides and below basal 4–5 segments, black setae dorsally on all tergites, becoming increasing abundant laterally and longer on apical 2–3 segments; sternites 5–6 with a few strong yellowish setae, stronger black bristles on sternite 7 and segment 8. Apical corners of tergite 9 (Fig. 8) slightly projecting posteriorly. Segments 8–9 shiny yellow brown. Sternite 8 (Fig. 9) short, membranous laterally on apical  $\frac{1}{3}$ , with a strongly produced median ridge, thickened posteriorly, membranous area bordered posteriorly by several strong black bristles.

Male unknown.

*Holotype* ♀. Bahamas, Rum Cay, 14–16 Feb. 1934. Utowana Exp. The holotype is in the MCZ collection. The specimen was formerly identified as *O. marginellus* (Scarborough and Rutkauskas, 1983).

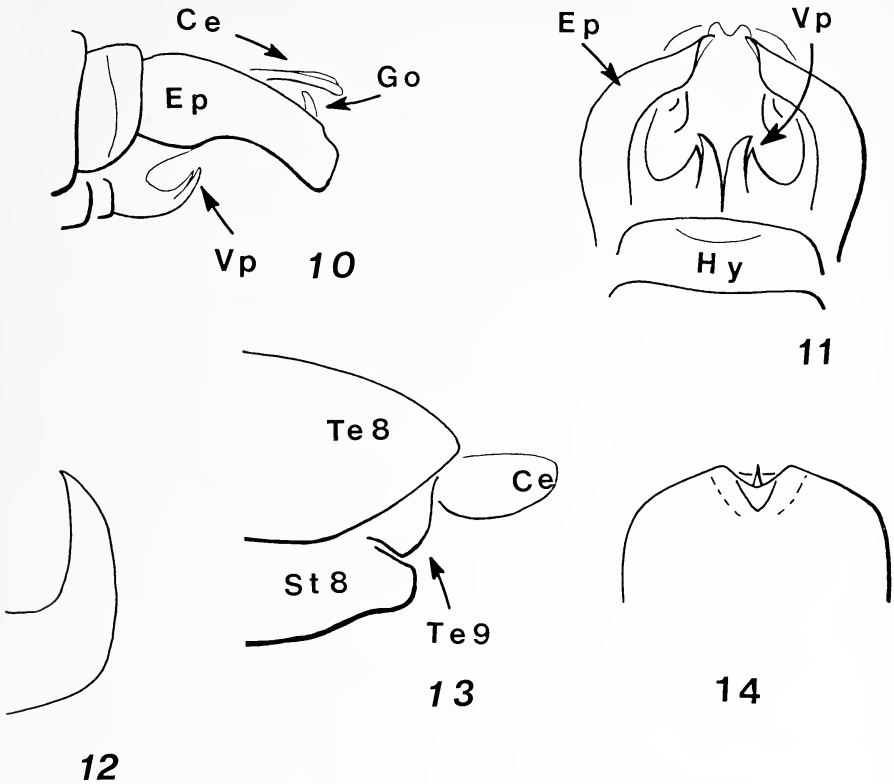
*Etymology.* The name *membranosus* refers to the membranous apical margin of sternite 8 in the female.

### ***Ommatius bipartitus*, new species**

Figs. 10–14

*Diagnosis.* *Ommatius bipartitus* is easily recognized by the bright brassy yellow facial pollen, the orangish to yellow facial bristles, 3rd antennal segment length about twice its width, 2 black postalar bristles; scutellum with 2 long, thin, bristly hairs; basal segment of hindtarsus wholly black or dark brown; most postocular and forecoxal bristles long and thin; costal margin straight and by details of the genitalia.

This species is similar to *O. piliferous* but is readily recognized by the characters listed above and by those in the discussion of the latter species. In addition, the male is quickly recognized by the apically truncate epandrium, the short hypandrium with its apically truncate margin, the gonostylus is sharply bent vertically near its base, and the gonocoxite has 2 strong basal teeth. In contrast, *O. piliferous* has an apically rounded epandrium and hypandrium, a dorsoventrally flattened gonostylus and a subovate gonocoxal plate.



Figs. 10–14. *Ommatius bipartitus*, genitalia: 10–12 male; 13, 14 female. 10. Lateral view. 11. Ventral view. 12. Gonostylus. 13. Lateral view. 14. Sternite 8.

**Description.** MALE: Length 14.0 mm. Face bright brassy yellow pollinose, front slightly lighter yellow, occiput yellowish. Bristles of face orangish to yellow, 1 or 2 on upper face with trace of brown; palp with whitish hairs basally, yellow to orangish apically, occipital pile white. Postoculars mostly pale orange or yellowish, 2 on 1 side black, 1–2 curved moderately forward, lateral postocular bristles longer and weaker than those above. Two ocellar and most antennal bristles dark brown or black, 3–4 on basal segment pale yellow. Style short, slightly less than  $1\frac{1}{4}$  times length of 3 basal antennal segments combined, 3rd antennal segment almost twice basal width.

Thorax dark brown, scutum mostly brown pollinose, brassy yellow behind humeral callus, light brown to yellowish in grooves, above wings, in prescutellar area and on margin of scutellum; postalar callus and base of scutellum reddish brown pollinose. Scutal bristles black, 2 notopleurals, 1 supra-alar, 2 postalars, 4 strong dorsocentrals posteriorly and numerous long, thin, brown or brownish hairs on sides in addition to the 2 rows of dorsocentrals anteriorly. Scutellum with scattered, fine pile dorsally

and 2 long, thin, brown marginal hairs. Pleuron mostly grayish pollinose, the an- and katapisternum yellowish, bristles pale orange. Halter reddish.

Wing hyaline, costal margin straight, stigma brownish, cells behind slight yellowish. R-m crossvein slightly before middle of discal cell, 1st medial cell constricted by  $\frac{1}{3}$  beyond middle,  $R_{4+5}$  forked at or slightly beyond base of 1st medial cell.

Coxae yellowish gray pollinose, bristles mostly pale yellow, those of forecoxa abundant, unusually long and thin, stronger and shorter on midcoxa, hindcoxa with 1 pale orange bristle. Femora slender, slightly reddish yellow to reddish basally, fore- and midtibiae yellow. Segments black as follows: apical  $\frac{1}{2}$  of fore and midfemora, apical two-thirds of hindfemur, apical three-fourths or more of hindtibia, fore- and midtibiae with narrow apical band. Basal segment of fore- and midtarsi mostly yellow, remaining segments blackish. Short hairs, including long bristles in ventral rows of fore- and midfemora, mostly yellowish, some black and setaceous in dark areas of femora and over general surface of tibiae. Mid-femur with 2 black bristles closely spaced in anteroventral row medially and 2 bristly yellow hairs basally; 1 blackish and 1 pale yellow bristle on apical  $\frac{1}{2}$  and 1 amber on basal  $\frac{1}{2}$  of anterior surface, 1 pale yellow postapical bristle. Hindfemur with 3 amber bristles anteriorly, bristles of anteroventral row short, all 4 amber on apical three-fourths; 8 amber bristles, evenly spaced, in posteroventral row almost twice length of those in anterior row. Bristles of tibiae and tarsi mostly black, 2-4 amber or yellowish on all tibiae and foretarsus.

Abdomen blackish brown to black with borders slightly reddish, brown pollen dorsally on all tergites and on sternites 5-7, yellow to yellowish gray on sides of all tergites and sternites 1-5. Pile and bristles on basal segments pale yellow or pale amber, noticeably bright yellow on sides of tergites 2-4 and base of 5; dorsal setae blackish on all tergites and sternites 5-8, setae longer on apical segments.

Genitalia (Figs. 10, 11) black to blackish brown with abundant black hairs on epandrium basally, hairs otherwise yellowish. Epandrium elongate, length about twice basal width, apical  $\frac{1}{3}$  only slightly tapered, apex truncate. Gonostylus (Fig. 12) with wide base, strongly curved vertically at basal  $\frac{1}{4}$ , moderately thick, tapered to point. Gonocoxite with basal process divided into 2 strong bladelike teeth. Hypandrium with apical margin truncate, median margin yellowish, otherwise black; fine, scattered, yellowish pile on apical  $\frac{1}{2}$ .

**FEMALE:** Similar to the male with the following differences; 15.5 mm, 8 postoculars and all antennal bristles black, r-m crossvein before middle of discal cell, constriction of 1st medial cell not noticeable. Hindfemur with only 6 bristles in posteroventral row; midtibiae with brown streak on apical  $\frac{3}{4}$  of the anterior surface. Genitalia (Fig. 13, 14) black, cercus pale reddish, tergite 9 with apical corners slightly projecting posteriorly. Sternite 8 with scattered blackish hairs, apical margin narrowly produced medially with a low ridge, the latter terminating in a prominent triangular mound and bordered by lateral grooves.

*Holotype* ♂ and *allotype* ♀. Cuba, Loma del Gato, Cobre Range, Ote. 3,000', July 3-7, 1936, Darlington collection. Paratype ♀, without abdomen; same data; ♀ Cuba, Osten Sacken collection, no further data. The types are in the MCZ.

*Variation.* The paratypes differ in that the facial pollen is a lighter brassy yellow and the strong bristles on the anterior surface of the midfemur are black whereas the postapical one is pale yellow. One female has only 4 postocular black bristles and a

few pale yellowish hairs below the 1st antennal segment. The other paratype has 5–6 long, brownish orange, facial hairs and 4–5 apical bristles in the ventral rows of the hindfemur are black.

*Etymology.* The name *bipartitus* refers to the division of the ventral gonocoxal process into two bladeli-like teeth.

### ***Ommatius hispidus*, new species**

Figs. 15–20

*Diagnosis.* *Ommatius hispidus* is very different from any species thus far described from the Caribbean region, particularly in the unusually strong bristles of the terminal segments of the abdomen, the predominantly yellow basal segment of the hindtarsus and the 2 preapical dorsal bristles and the postero-ventral discontinuous row of bristles on the hindfemur. In addition, the absence of a produced costal margin, the presence of a swollen hindfemur, a long spine on the hindtibia and an unusual genitalia readily distinguishes the male from other species.

*Description.* MALE (teneral): Length 14.0 mm, face and occiput slightly yellowish gray pollinose, front grayish. Papal and facial hairs pale yellow to whitish, occipital pile white; 3–7 postoculars plus 1–2 long bristles behind, 2 ocellar and most antennal bristles black, 3–4 pale yellow hairs below antennal segment 1. Style about 1½ times length of basal 3 antennal segments combined, 3rd segment length almost twice its width.

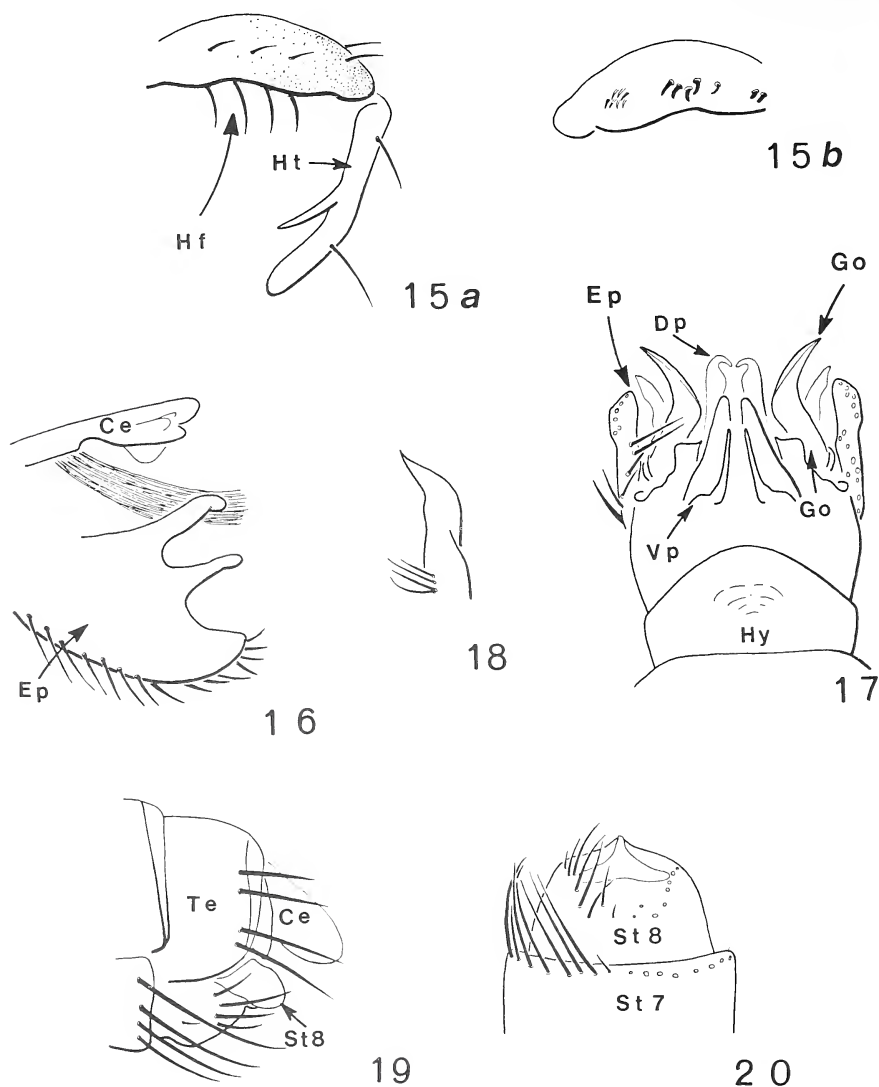
Scutum mostly brown pollinose, pale brassy yellow behind humeral callus, pale brown to yellowish elsewhere including scutellum. Scutum with an anterior light brown pollinose longitudinal stripe. Scutal bristles black, 2 notopleurals, 1 supra-alar, 1 postalar and 2 strong dorsocentrals posteriorly, numerous scattered, weak, brown hairs on sides above wings; scutellum with scattered pale pile and 5–6 weak, brown hairs on margin, about same length as dorsal pile. Pleuron mostly grayish pollinose, anepisternum yellowish, bristles pale yellow. Halter yellow.

Wing hyaline, costal margin not dilated, r-m crossvein before middle of discal cell; 1st medial cell constricted by less than ⅓ beyond middle,  $R_{4+5}$  forked at or slightly before base of 1st medial cell.

Coxae gray pollinose, bristles stiff and whitish. Legs and vestiture mostly yellowish, slightly brownish to black as follows: apical ⅓ completely and basal ⅓ of forefemur anteriorly, apical two-thirds of midfemur and hindtibia, apical ½ of hindfemur, narrow apices of fore- and midtibiae, apical ⅓ of anterior surface of hindtibia; basal segment of all tarsi mostly yellowish, hindtarsus slightly brownish yellow. Forefemur with 1 anterior weak bristle basad, ventral bristles long and yellowish. Midfemur with most bristles yellowish, 1 black anteriorly; ventral bristles somewhat long and strong. Tibial bristles mostly yellowish, midtibia with 1 black anteriorly. Foretarsus with 1 yellowish bristle, all others black. Hindfemur (Fig. 15) swollen with 4 strong yellowish bristles in anteroventral row, none on basal or apical ¼; posteroventral row discontinuous with 2 strong, peglike, black bristles basally, 5 black bristles clustered medially and a patch of several setaceous yellowish hairs apically; 3 yellowish bristles anteriorly plus 2 preapical, 1 of latter more posteriorly. Hindtibia arcuate with 1 thick, long, spine medially and 2 long yellowish bristles laterally.

Abdomen with pile and setae yellowish on sides of tergites and sternites below,





Figs. 15–20. *Ommatius hispidus*, genitalia and hindleg: 15–18 male; 19, 20 female. 15. Hindleg, anterior view (a.), hindfemur, posterior view (b.). 16. Lateral view. 17. Ventral view. 18. Gonostylus. 19. Lateral view. 20. Sternites 7–8. Abbreviations: Hf = hindfemur, Ht = hindtibia, Dp = dorsal process.

black setae and hairs on all tergites dorsally becoming abundant and replacing lighter hairs on apical segments. Sternites 7 and 8 with abundant yellowish bristly hairs on apical margins, 1 strong bristle laterally on sternite 8.

Genitalia (Figs. 16, 17) elongate, brown to brownish yellow, with mostly setaceous and thin yellowish hairs; a dense patch of extremely, long, yellowish hairs below

cercus basally. The latter reaching or slightly exceeding apical margin of epandrium and cercus. Hypandrium broadly rounded apically, slightly conical basally, the base with abundant short, thin, brownish hairs. Epandrium flattened laterally, basal height as great as or slightly greater than length, the narrow ventral and posterior margins with numerous, black, setaceous hairs; the apical margin with 2 flat, slender, processes and a thick ventroapical lobe, the inner margin with several dark, strong, bristles. Gonostylus (Fig. 18) flat, elongate and horizontal, the apical  $\frac{1}{3}$  only slightly curved vertically. Gonocoxite with a bifid ventral process, the larger somewhat flattened dorsoventrally and broad basally, the shorter branch daggerlike and flattened laterally. Two additional dorsal processes above aedeagus, somewhat flattened laterally and about as long as gonostylus.

**FEMALES:** Lengths 14.5–15.5 mm. Thorax and abdomen dark brown to black. Scutellar margin with 2 weak, brownish hairs. Postapical bristle of midfemur black; hindfemur slender with 5–6 bristles in anteroventral row, the apical 3–4 noticeably stronger and longer than basal 2, row short, extending to apical  $\frac{1}{3}$  of segment; posterior row discontinuous with 2 long bristles basally, 2 at middle and several setaceous hairs clustered apically, 2–3 often stronger than others. Foretibia with black bristles apically only, ventral row of fine hairs partially black; mid- and hindtibiae with 2–3 black bristles beyond the apex. Hindtibia without strong spine.

Abdomen dark brown to black, apical tergites sooty red, reddish brown to pinkish pollinose dorsally, yellowish gray on sides and below. Segments 7–8 (Figs. 19, 20) with several, long, black bristles, unusually strong on sternite 7 apically, apical corners of tergite 8 and sternite 8 basally. Sternite 8 thick medially with a strong apical rounded ridge, a wide membranous triangle behind ridge, the latter margined posteriorly by a V-shaped row of strong black bristles.

*Holotype* ♂. Cuba, Stego de Los Vegas, A. Otero. *Allotype* ♀. Pan de Matanzas Mts., June 12, 1932, colls. S. C. Bruner, A. R. Otero, L. C. Scaramuzza (S. W. Bromley collection). *Paratype* ♀, Cuba, no further data. The types are in the USNM.

*Etymology.* The name *hispidus* refers to the strong bristles on the apical segments of the abdomen of both sexes.

### *Ommatius marginellus* (Fabricius)

*Asilus marginellus* Fabricius, Species Insectorum, II, p. 464, 1781; Mantisse Insectorum, II, p. 178, 1787. Type locality Virgin Islands, St. Croix. Type ♀, Kieler Collection, Copenhagen, Denmark.

*Dasyopogon marginellus*; Wiedemann, Diptera Exotica, I, p. 213, 1821.

*Ommatius marginellus*; Coquillett, 1910:579. Designated type species; Wolcott, 1948, vol. 32, p. 453; Hull, 1962, Bull. 224, pt. 2, pp. 434–436; Farr, 1965:19–25. Removed from list of asilids from Jamaica; Martin and Papavero, 1970:59.

*Discussion.* Beyond the brevity of the original description of *O. marginellus* (Fabricius, 1781), a major error resulting in the misidentification of the species is a statement in the literature (Curran, 1928; Bromley, 1929) that *O. marginellus* possesses 2 marginal scutellar bristles. Furthermore, Bromley (1929) stated that Cuban specimens of *O. marginellus* had brown mid- and hindtarsi. I examined several Cuban specimens that carry Bromley's identification labels with the name *O. marginellus*, and none had a wholly brown midtarsus. The basal segment of the hindtarsus is

almost entirely yellowish in most specimens, and weak scutellar hairs are present in some cases but are absent in others. Upon examination of the male type, I found an absence of scutellar bristles, or scars associated with them, and the basal segment of the midtarsus is mostly yellowish on the basal half or more. Thus the Cuban specimens referred to by Bromley (1929) as *O. marginellus* do not belong to that species, and I propose to remove the name of *O. marginellus* from the list of species of Asilidae from Cuba. Most of the specimens used in this study were originally identified (carry an identification label) by Bromley as *O. marginellus*.

#### ACKNOWLEDGMENTS

The following contributed specimens used in this study: Norman Woodley, Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, Massachusetts; Pedro Wygodzinsky, American Museum of Natural History (AMNH), New York; Lloyd V. Knutson and Raymond Gagné, Systematic Entomology Laboratory, USDA, Washington, D.C. Thanks are also due to the staff of the Diptera section in the Systematic Entomology Laboratory, USDA, at the United States National Museum (USNM), who provided working space, gave helpful suggestions and encouragement during this study; to Eric Fisher, Department of Food and Agriculture, Sacramento, California, for reviewing and making helpful suggestions on an early draft of the manuscript; to the Towson State University Faculty Research Committee for support of this study; and Keith Harris, Department of Biological Sciences, Towson State University, for preparing the figures.

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## REVIEW OF THE CARIBBEAN *GERON* MEIGEN (DIPTERA: BOMBYLIIDAE)

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**Abstract.** —Seven new species plus one previously known species of *Geron* Meigen are reported from the northern and central Caribbean Islands. *Geron insularis* Bigot is synonymized with *G. senilis* (F.). *Geron senilis* is redescribed from new material and a lectotype is designated for the species. New species are described, illustrations of significant characters and a key to the species are included.

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*Geron senilis* (Fabricius) and *G. insularis* (Bigot) are the only species of *Geron* Meigen reported from the Caribbean Islands (Painter et al., 1978). Unfortunately, descriptions of the 2 species (Fabricius, 1794; Wiedemann, 1828; Bigot, 1857) are brief, and lack adequate characters to separate the species (Painter, 1932). Recently Painter and Painter (1962) located 3 specimens of *G. senilis* in the Lund and Sehestedt collection in Denmark (these are part of the Fabrician syntype series; L. Lyneborg, pers. comm.) but did not clarify the status of the species. They also located the Bigot syntype series of *G. insularis* in the Paris Museum, selected a male lectotype (labeled "*Bombylius insularis*, type, Cuba") and a female lectoallotype (labeled #242, ♀), and gave a redescription of the species. However, the redescription lacks sufficient characters to separate *G. insularis* from *G. senilis* or other species in the Caribbean Islands.

To resolve the problem, we studied the 5 Fabrician syntypes of *G. senilis* and the lectotype of *G. insularis*. Loïc Matile of the Paris Museum removed the male genitalia from the male lectotype of *G. insularis* and sent it to us for examination.

Of the 5 syntypes of *G. senilis*, the one in the Kieler collection is badly damaged and is of no value in determining the species identity. The 4 syntypes (2♂♂, 2♀♀) in the Lund and Sehestedt collection are in better condition although the pile is virtually absent in 2 specimens and discolored in a third. Two males have their genitalia sufficiently exposed for comparison. One male has the genitalia expanded and the other has it closed. One male bears a handwritten label with the name "*B. senilis*," and a female has a locality label with "var. a ins. thoma."

Comparison of the 2 male syntypes of *G. senilis* clearly shows them to be the same species. The male, with the expanded genitalia and unlabeled, has slender structures and may appear slightly underdeveloped upon initial examination. However, the genitalia of *G. senilis* are quite simple and differ significantly from those of the more robust, structurally complicated, Nearctic species. The syntype male, in the best condition with closed genitalia and the label "*B. senilis*," is designated LECTOTYPE for *G. senilis*.



We also studied a series of about 150 specimens of both sexes which were collected from the islands in the Bahamas southward to Jamaica and eastward to the Virgin Islands. The series included the female lectoallotype and the genitalia of the male lectotype of *G. insularis* and several specimens identified as *G. insularis* by Painter. We compared these specimens with the syntypes of *G. senilis* and found them to be virtually identical. We therefore conclude that the male lectotype of *G. insularis* is conspecific with the lectotype of *G. senilis*, and thus the two taxa are synonymous. However, the former lectoallotype of *G. insularis* is clearly not a female of *G. senilis*. It differs significantly in the vestiture of the head and dorsum of the thorax and abdomen to distinguish it from *G. senilis*. Since we were unable to dissect the female, a description of the species must be delayed until additional material becomes available.

While working on this problem, we found 7 new species of *Geron* Meigen from the northern and central Caribbean Islands. This study also reports these species and provides a key to the known species from this region.

KEY TO SPECIES OF *Geron* MEIGEN IN THE CARIBBEAN

- 1. Pile of 2nd antennal segment white ventrally ..... 2
- Pile of 2nd antennal segment wholly black or brown ..... 3
- 2. Pile of 2nd antennal segment yellowish and brown dorsally, white ventrally; apical process of gonocoxite somewhat robust (Fig. 33), aedeagus long (Fig. 34); arms of vaginal apodeme kidney-shaped apically (Fig. 32c) (Cuba) .. *G. nephroideus*, new species
- Pile of 2nd antennal segment wholly white; apical process of gonocoxite slender (Fig. 1a), aedeagus short (Fig. 1b); arms of vaginal apodeme flat and laminate apically (Bahamas, Greater Antilles) ..... *G. senilis* (Fab.)
- 3. Hindfemur reddish, basal antennal segment with wholly brownish (♂) or mostly yellowish (♀) pile (Jamaica) ..... *G. farri*, new species
- Hindfemur dark brown to blackish, basal antennal segment with variable pile ..... 4
- 4. Basal antennal segment with mostly dark pile dorsally ..... 5
- Basal antennal segment with mostly whitish or yellowish pile dorsally ..... 7
- 5. Gonostylus and vertical plate fused, slightly longer than apical process (Fig. 22); gonocoxite lobed medially with several spatulate fingers (Fig. 23) (Antigua) ..... *G. binatus*, new species
- Gonostylus and vertical plate separate, both shorter than apical process; gonocoxite not lobed medially, spatulate fingers absent ..... 6
- 6. Gonostylus long and slender, articulated near base of apical process; vertical plate large with a long basal spine (Figs. 6–10) (Bahamas) ..... *G. salmonus*, new species
- Gonostylus short, articulated near apex of vertical plate; vertical plate small with a short spine (Figs. 29–31) (Dominican Republic) ..... *G. articulatus*, new species
- 7. Basal antennal segment with wholly whitish pile; vertical plate, gonostylus and apical process of gonocoxite slender and noticeably weak (Figs. 26, 27); aedeagus short, not noticeably projecting (Fig. 28) (Antigua) ..... *G. declinatus*, new species
- Basal antennal segment usually with several dark hairs dorsally; vertical plate, gonostylus and apical process noticeably large and strong (Figs. 18–20); aedeagus long, usually projecting near tip of apical process (Fig. 19) (Bahamas, Cuba) ..... *G. exumae*, new species

*Geron senilis* (Fabricius)

Figs. 1-6

*Bombylius senilis* Fabricius, 1794:411. Type locality, Americae Meridionalis Insularis. Lectotype ♂, Lund and Sehestedt Col., Universitetets Zoologiske Museum, Copenhagen, Denmark.

*Geron senilis*: Weidemann, 1828:357; Johnson, 1908:72; 1913:58; Painter, 1932: 144, 165, 166; Painter and Painter, 1962:48; Hull, 1973:204, 206; Painter et al., 1978:17.

*Geron insularis* (Bigot): Painter and Painter, 1962:47-48, designated ♂ lectotype, redescribed species based upon lectotype. Type locality Cuba, lectotype ♂, Paris Museum. **NEW SYNONYMY.**

*Diagnosis.* *Geron senilis* is easily recognized by its white oral margins; pile and hairs of head, antenna and abdomen white; front entirely and legs usually with silvery scales and hairs, ocellar hairs whitish to pale yellowish and the slender male genitalia.

*Geron senilis* is easily recognized from other Caribbean species by the characters of the genitalia and the white vestiture of the antenna and head. The scales and pile of the front are entirely white in females of *G. senilis*. In other species, the fronts of females have numerous yellow to golden scales and a few to several yellowish hairs.

*Description.* Males: Length 2.2-4.9 mm, wing 1.9-4.3 mm, proboscis 1.2-2.5 mm, front at antennal base 0.1-0.4 mm, antennal ratios 1.8:1.0:6.0 to 2.0:1.0:7.0. Ground color mostly black, oral margin whitish; apical corners of tergite 1 broadly and corners of tergites 2-4 and cercus narrowly yellowish. Gonocoxite 9 brown basally, shiny black to dark brown apically.

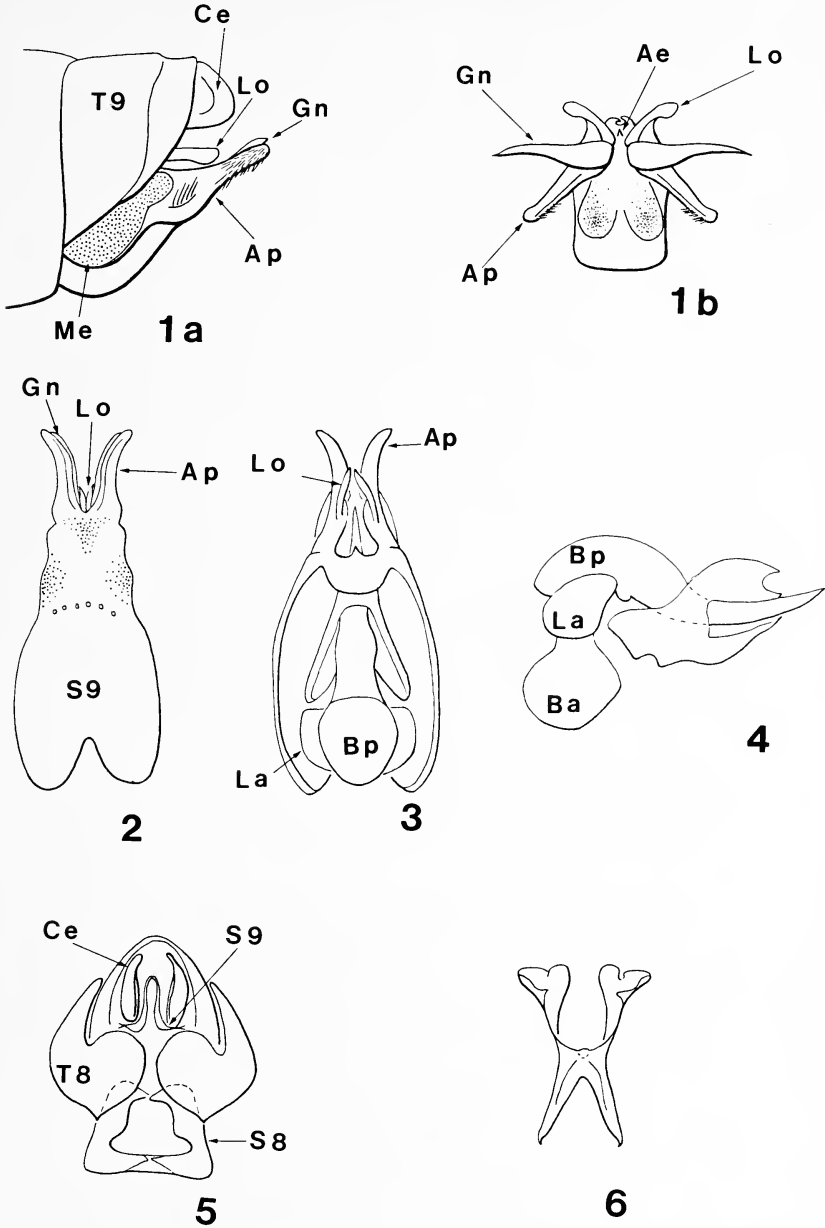
Face, front and lower ½ or more of occiput gray pollinose with white pile and silvery scales, occiput blackish brown pollinose dorsally with mostly white pile, ocellar tubercle with pale yellowish or yellowish white pile, golden scales posteriorly. Antenna grayish pollinose with basal 2 segments white pilose.

Scutum black pollinose, slightly brownish anteriorly and laterally, 2 grayish pollinose stripes anteriorly; anterior ⅓ with long, dense, white pile and mostly yellowish to silvery flat scales, posterior two-thirds with pile shorter, less dense and often pale yellow to pale yellowish brown; scales scattered, golden yellow and decumbent; a few stiff yellowish hairs laterally and posteriorly. Scutellum blackish pollinose with white pile and silvery scales, anepimeron and meron bare or nearly so.

Wing hyaline, subcostal cell slightly yellowish, veins brownish yellow, node of vein M similar in color to surrounding veins. R-m crossvein beyond middle of discal cell; vein between discal and 1st medial cells slightly sinuous to straight; anal cell closed, stalk of anal cell slightly more than length of r-m crossvein. Costal vein with white pile basally; squama and fringe white. Halter creamy white.

→

Figs. 1-6. Genitalia of *G. senilis*; 1-4 male, 5, 6 female. 1a, Closed condition, lateral view; 1b, expanded condition, apical view. 2. Gonocoxite plus sternite 9, ventral view. 3. Aedeagus and gonocoxite, dorsal view. 4. Aedeagus, lateral view. 5. Sternite 8, and lobes of tergite 8,



ventral view. 6. Vaginal apodeme, ventral view. Abbreviations: Ae = aedeagus, Ap = apical process of gonocoxite, Ba = basal ejaculatory apodeme, Bp = basal point of aedeagus, Ce = cercus, Dr = anterior arms of dorsolateral apodeme of aedeagus, Lo = lobe of gonocoxite, Me = membrane, S = sternite, Sh = sheath, Sp = spine of vertical plate, T = tergite, Vp = vertical plate.

Legs white pilose, with mostly white scales; femora sometimes with sparse brownish scales apically; spines of tibiae dark brown.

Abdomen black pollinose, with traces of brown laterally, gray ventrally, pile generally white, sometimes faintly yellowish; dorsal scales yellow and curved, silvery and flat laterally and ventrally.

Genitalia (Figs. 1–4). Gonocoxite with large oval membrane laterally and a horizontal, apically rounded, dorsal process or lobe; the apical process slender, pilose on apical half or more, and slightly convex apically. Gonostylus slender, almost as long as apical process. Aedeagus slightly undulate, narrowly connected to gonocoxite via dorsolateral ramus, base of aedeagus and basal apodeme ovate, apex short, not clearly exposed in either expanded or closed condition.

Females: Lengths 2.5–4.6 mm, wing 2.5–4.6 mm, proboscis 1.2–2.5 mm, front 0.2–0.5 mm, antennal ratio 2.2:1.0:5.8 to 2.0:1.0:6.0. Oral margin sometimes slightly yellowish, usually white; front with silvery scales and white pile; scutal dorsal stripes less defined than in males, dorsum of scutum and abdomen often brownish black pollinose.

Genitalia. Tergite 8 with oval lobes, slightly longer than wide, with 5–6 short bristles ventrally. Sternite 8 slightly longer than wide, rhomboid-shaped, weakly setaceous apically, middle membranous and bell-shaped (Fig. 5). Vaginal apodeme with dorsal arms somewhat lamellate apically (Fig. 6). Sternite 9 narrow, weakly sclerotized, extending upward between cerci basally.

*Lectotype*. ♂, 1♂ and 2♀♀ paralectotypes, Lund and Sehestedt Collection; 1 paralectotype (sex ?), Kieler Collection; Universitetets Zoologiske Museum, Copenhagen, Denmark.

*Other specimens examined*. Cuba 3♂♂; Puerto Rico 3♂♂, 3♀♀; Mona Island ♂, ♀; Virgin Islands (St. Thomas) ♀; Turks and Caicos Islands 5♂♂, 4♀♀; Jamaica 5♂♂, 5♀♀; Bahama Islands (Exuma, San Salvador, Eleuthera, Berry, North Bimini, Long) 140♂♂, 25♀♀.

*Distribution*. *Geron senilis* is active through its range from December to August. Its range extends from the Bahamas southward to Jamaica and eastward to the Virgin Islands.

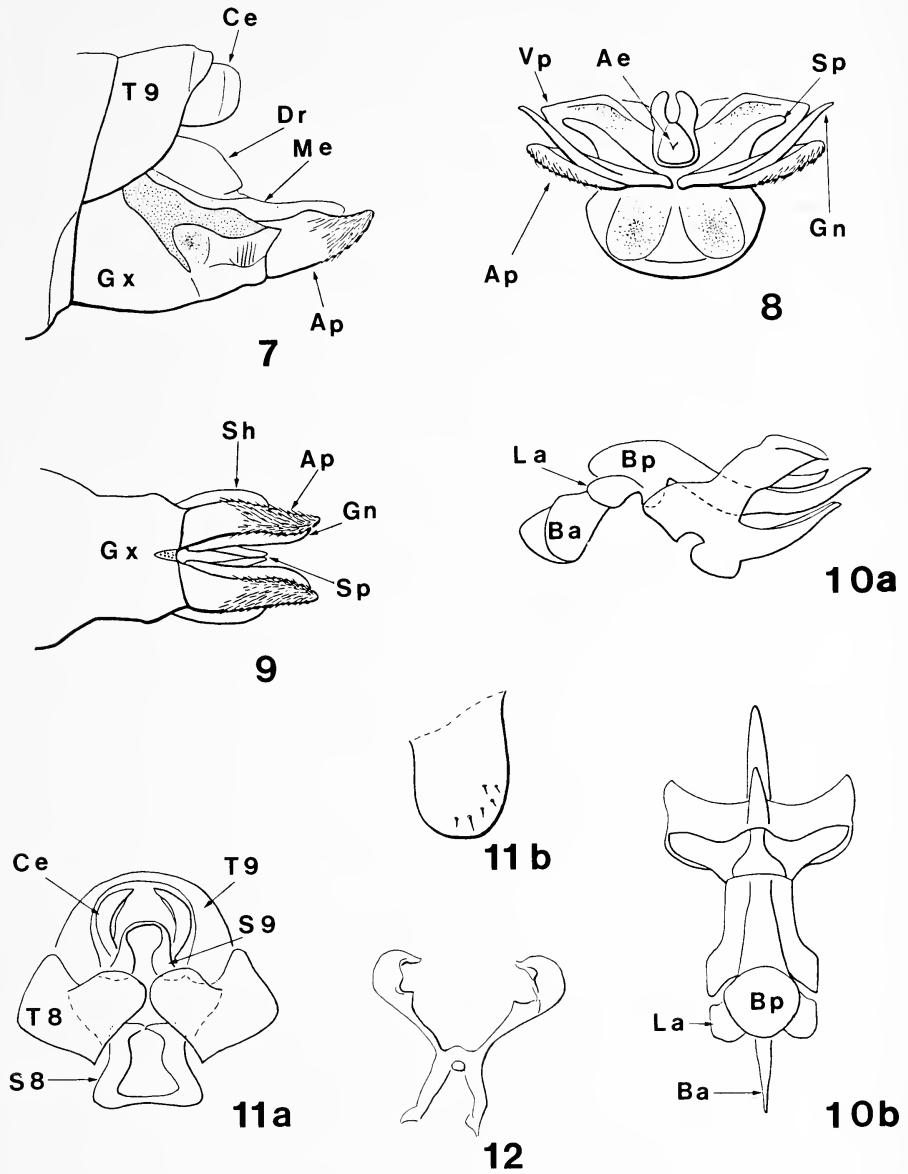
### ***Geron salmonus* Scarbrough and Davidson, new species**

Figs. 7–12

*Diagnosis*. *Geron salmonus* is recognized by its usual pinkish oral margins, basal antennal segment with mostly dark pile dorsally, 2nd antennal segment black pilose, apical ½ of each femur with abundant brownish scales and several stiff brown hairs; vertical plate of male genitalia with a long, strong spine; female with abundant frontal golden scales and brownish pile, vaginal apodeme with dorsal arms clavate.

*Geron salmonus* is similar to *G. farri*, new species but can be distinguished by its whitish frontal vestiture, presence of whitish pile ventrally on the basal antennal segment and the vertical plate with a long basal spine.

*Description*. Male holotype. Length 5.8 mm, ground color largely black, oral margin pinkish or salmon-colored. Gonocoxite reddish brown basally, shiny black apically. Femora dark brown to blackish, tibiae yellowish brown to brown with the midtibia lightest.



Figs. 7-12. Genitalia of *G. salmonus*; 7-10 male, 11, 12 female. 7. Closed condition, lateral view. 8. Expanded condition, apical view. 9. Closed condition, ventral view. 10. Aedeagus, lateral (a) and dorsal (b) views. 11. Ventral view (a) with lobe of tergite 8 (b) enlarged, showing setae on inner surface. 12. Vaginal apodeme.



Face, front and lower  $\frac{1}{2}$  of occiput gray pollinose with white pile and silvery scales, front with scattered pale yellowish scales. Upper  $\frac{1}{2}$  of occiput black pollinose with mostly white pile; dorsal postocular pile slightly yellowish. Ocellar tubercle with abundant blackish pile, a few golden scales posteriorly. First antennal segment with mostly dark pile dorsally, white ventrally; 2nd segment dark pilose. Antennal ratio 2.7:1.0:6.0, proboscis length 2.9 mm, front 0.4 mm at antennal base.

Scutum mostly black pollinose dorsally, gray anteriorly including 2 admedian stripes and laterally; posterior callus brownish gray pollinose. Anterior  $\frac{1}{3}$  of scutum with mostly white pile and yellowish white scales; posterior two-thirds with scales curved and golden, pile shorter, less dense and blackish brown; posterior margin with scattered long yellow pile. Scutellum black pollinose with yellow pile and scattered golden scales, apical margin weakly brown pollinose. Pleuron gray pollinose with silvery scales and white pile, anepimeron and meron bare.

Coxae gray pollinose with white pile and silvery scales. Femora mostly white pilose and tomentose; apical  $\frac{1}{2}$  of each femur with brownish scales anteriorly and several brownish hairs. Foretibia with brownish scales entirely, mid- and hindtibiae with brownish anteriorly and white scales posteriorly. Tibial spines black.

Wing 5.0 mm, hyaline, subcostal cell weakly yellowish. Veins brownish yellow; node of vein M slightly darker than surrounding veins; r-m crossvein at or slightly beyond middle of discal cell. Discal cell crossvein sinuous apically, stalk of anal cell about  $\frac{1}{2}$  length of r-m crossvein. Squama whitish, fringe whitish pilose; costal vein with pale yellowish pile basally. Halter yellowish.

Abdomen black pollinose dorsally with traces of brown, gray laterally and ventrally, brown most apparent on posterior 4–5 segments. Abdomen mostly whitish pilose, posterior 3–4 segments with several stiff yellow and brownish to blackish hairs. Gonocoxite thinly pollinose basally with a row of pale yellowish to brownish hairs.

Genitalia (Figs. 7–10). Gonocoxite large, slightly convex in lateral view, basolateral membrane white and V-shaped; apical process with abundant pale yellowish pile. Vertical plate large, with a prominent basal spine, and connected to a whitish membrane or sheath dorsally. Dorsolateral ramus ("hypovalve" of Painter, 1932) of gonocoxite broadly joined to aedeagus, exposed below epandrium as an apically pointed sclerotized plate. Gonostylus slender, slightly shorter than apical process. Aedeagus broad basally and subtriangularly rounded, shaft broadly U-shaped, apex not noticeably exposed when genitalia are expanded. Aedeagal apodemes as in Figure 4.

Female allotype. Differs from male as follows: length 5.1 mm, wing 4.9 mm, proboscis 2.3 mm, antennal ratio 2.3:1.0:5.7. Front grayish to brown pollinose with abundant yellowish brown pile and mostly golden scales, silvery scales along eye margin and above antenna. Upper occiput brownish black pollinose with golden scales, abundant behind ocellar tubercle; postocular pile yellow, yellowish white posteriorly. Dorsum of thorax and abdomen with dense brownish pollen and pile, pile darker yellow than in male.

Genitalia (Figs. 11, 12). Tergite 8 with rounded lobes ventrally, inner margin with 5–6 evenly spaced setae. Sternite 8 rhomboid-shaped, middle membranous and bell-shaped, weakly spinous apically. Vaginal apodeme with dorsal arms clavate. Sternite 9 broad basally, narrow apically, extending between cerci.

Variation. Length ♂ 5.1 to 6.4 mm, ♀ 3.5 to 5.4 mm; wing ♂ 4.3 to 5.4 mm, ♀ 3.3 to 5.0 mm; proboscis ♂ 2.5 to 2.9 mm; ♀ 1.9 to 2.9 mm; front ♂ 0.4 to 0.5 mm; ♀ 0.3 to 0.4 mm; antennal ratio ♂ 2.7:1.0:5.3 to 2.7:1.0:6.7, ♀ 2.3:1.0:5.7 to 2.5:1.0:4.8. Oral margin usually pinkish, rarely whitish. Males usually have some pale yellowish scales on the front, rarely entirely silvery; golden scales are usually absent on the occiput. The brown pollen on the dorsum is usually in trace amounts only in males.

*Type material.* Holotype. ♂, San Salvador (Watlings) Island, Bahamas, scrub growth, 8.VI.1981, H. Oestreicher. Allotype. ♀, same location, 5.VI.1981, D. Davidson; both are in the U.S. National Museum, Washington, D.C. Paratypes 23♂♂, 22♀♀, same location as types, 2–15.VI.1978, 2.VI.1979, 3–5.VI.1980, 29.V–15.VI.1981, various collectors. Paratypes are in the U.S. National Museum; American Museum of Natural History, New York; Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; Universitetets Zoologiske Museum, Copenhagen, Denmark; Entomological Museum, University of California, Riverside, California; and Museum of Zoology, Towson State University, Baltimore, Maryland.

*Etymology.* The specific name *salmonus* refers to the pinkish-colored oral margins.

### ***Geron farri* Scarbrough, new species**

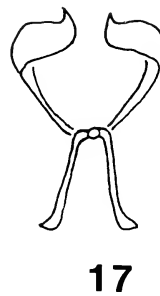
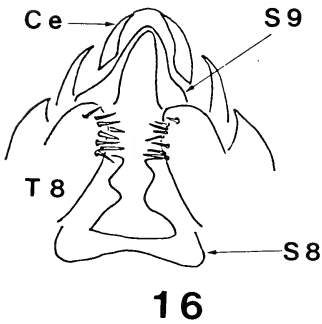
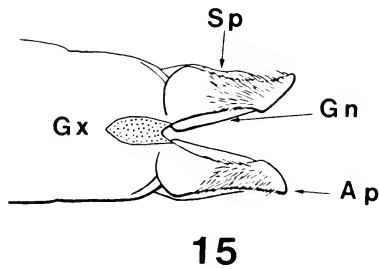
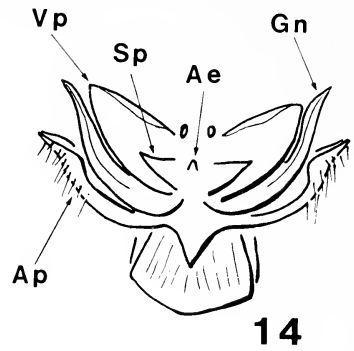
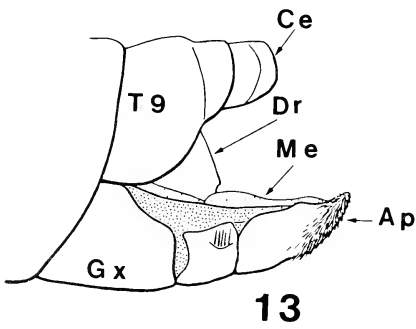
Figs. 13–17

*Diagnosis.* *Geron farri* is recognized by its white oral margin; basal 2 antennal segments with wholly dark pile (♂) or mostly yellow pile (♀) with several dorsoapical dark hairs; front with brown pile and golden to brownish scales; anterior and dorsal ½ or more of each femur apically with brownish scales and several brown hairs; apical 3–4 abdominal segments with numerous brown hairs; hindfemur reddish; vaginal apodeme of females with dorsal arms clavate, apical ¼ of apical gonocoxal process of males slightly projecting around apex of gonostylus; vertical plate with short basal spine.

*Geron farri* is similar to *G. salmonus*, new species but is readily identified by its brownish or yellowish antennal pile, the brownish to yellowish pile and tomentum of the front, the reddish hindfemur and detailed characters of the genitalia.

*Description.* Male holotype. Length 5.2 mm. Ground color dark brown to black, oral margin white; gonocoxite reddish brown basally, shiny brownish medially, brownish black to black laterally and apically. Femora, especially hindfemur, reddish to reddish brown; tibiae yellowish brown.

Face and lower ½ of occiput grayish pollinose with white pile and silvery scales, front with golden scales and brown pile, antennal pile brownish. Ocellar pile dark brown to golden brown, a few dorsal postocular hairs lighter brown. Upper ½ of occiput velvety black pollinose, brownish gray laterally above wings and on anepisternum, remaining pleuron and scutum grayish anteriorly, including 2 short admedian dorsal stripes. Anterior ⅓ of scutum with dense white pile and scattered white scales, posterior two-thirds with scattered golden scales and shorter, less dense, blackish pile; a few bristly yellowish hairs laterally above wings and along posterior margin. Scutellum with whitish pile dorsally, longer yellowish hairs along margin. Pleuron with white pile and scales, anepimeron and meron bare.



Figs. 13–17. Genitalia of *G. farri*; 13–15 male, 16, 17 female. 13. Closed condition, lateral view. 14. Partial expanded condition, apical view. 15. Closed condition, ventral view. 16. Ventral view. 17. Vaginal apodeme.

Coxae gray pollinose with white pile and silvery scales. Femora apically with abundant brownish scales on anterior and dorsal  $\frac{1}{2}$  or more, whitish elsewhere; tibiae with mostly brownish scales, some brown scales intermixed with white. Femora with mostly white hairs; apical  $\frac{1}{5}$  of each femur and anteroventral row of midfemur with brown hairs. Tibial spines brownish to black.

Wing 5.1 mm, sharply angular apically, hyaline, subcostal cell yellowish. Veins yellowish, node of vein M with a dark spot, r-m crossvein beyond middle of discal cell and about same length as anal stalk; vein between discal and 1st medial cells sinuous. Squama and fringe whitish. Costal vein with yellowish pile basally. Halter yellowish.

Abdomen with velvety black pollen and golden scales dorsally, gray pollinose with silvery scales ventrally; pile primarily pale yellowish dorsally and white ventrally; apical 3–4 segments with numerous brown to blackish bristly hairs. Gonocoxite thinly brown pollinose basally, with a row of pale yellowish hairs.

Genitalia (Figs. 13–15). Gonocoxite large, slightly convex in lateral view, with a wide T-shaped whitish membrane basolaterally, apical process with abundant brownish pile, apical  $\frac{1}{4}$  with inner margin slightly angular and curved around apex of gonostylus; dorsolateral ramus broadly joined to aedeagus, apically subtruncate, often projecting as a wide sclerotized plate below epandrium. Gonostylus moderately thick basally, slender along most of its length, about as long as apical process. Median vertical plate with a short basal spine, about  $\frac{1}{2}$  to  $\frac{1}{5}$  length of apical process; dorsal margin sharply curved medially, attached to brownish sheath or membrane that covers and extends slightly beyond apical process laterally. Aedeagus almost identical to that of *G. salmonus*; basal point of aedeagus rhomboid, shaft strongly bent downward basally, aedeagus not noticeably projecting when genitalia are expanded.

Female allotype (Figs. 16, 17). Differs from male as follows: length 5.7 mm, proboscis 2.9 mm, front 0.5 mm, wing 5.6 mm, antennal ratio 2.5:1.0:6.5. Basal antennal segment mostly yellowish pilose, several dorsoapical hairs brownish. Front with mostly golden scales and brownish yellow to brown hairs, white scales bordering eyes near antenna. Upper  $\frac{1}{2}$  of occiput with abundant golden scales and yellowish pile. Scutum and abdominal dorsum with abundant dark pile in addition to yellow. Tergite 8 with 8–9 irregularly spaced stiff setae; sternite 8 slightly rhomboid-shaped with a median bell-shaped membrane. Vaginal apodeme with dorsal arms flat and clavate.

Variation. ♂ length 3.7 to 5.2 mm, proboscis 2.0 to 3.0 mm, wing 3.6 to 5.0 mm, antennal ratio 2.9:1.0:5.0 to 3.2:1.0:6.0, front 0.4 to 0.5 mm. Squama and fringe sometimes yellowish and the anterior surface of the hindfemur usually has several brown hairs. The femora are usually reddish brown to reddish yellow.

*Type material.* Holotype, ♂, Jamaica, B.W.I., St. Thomas, 4 mi woods, 15.VI.1954, T. H. Farr. Allotype ♀, Jamaica, Linguanea Plain, ?XI.1911, C. T. Brues. Paratypes. 2♂♂, St. Thomas, 14 mi E Kingston on Mount Bay Rd., 28.V.1954, on *Croton humilis* L., T. H. Farr; ♂, St. Andrew, Hermitage Dam, 30.V.1954, T. H. Farr; ♂, Kingston, date ?, C. W. Johnston. The holotype and 3 paratypes are in the Museum of the Institute of Jamaica, Kingston. The allotype and 1 paratype are in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

*Etymology.* *Geron farri* is named after T. H. Farr for his contributions to Jamaican dipterology.

***Geron exumae* Scarbrough, new species**

Figs. 18–22

**Diagnosis.** *Geron exumae* is recognized by its creamy white to yellowish oral margin; basal antennal segment mostly white to pale yellowish pilose, several brownish hairs dorsoapically, 2nd segment usually brown pilose; front with mostly whitish scales in males and golden scales in females; femora mostly with white scales and pile, forefemur with apical  $\frac{1}{3}$  to  $\frac{1}{2}$  brown tomentose; male with apical process short and narrow, dorsolateral ramus acutely angular apically, vertical plate with a short basal spine; and female with dorsal arm of vaginal apodeme flat and apically clavate.

*Geron exumae* is similar to *G. salmonus*, new species and *G. farri*, new species but is recognized by its usual smaller size, prominent white to yellowish antennal pile, and details of the male and female genitalia. In addition, *G. exumae* has a dark brown hindfemur whereas it is reddish in *G. farri*.

**Description.** Male holotype. Length 3.4 mm. Ground color dark brown to black; lower face, narrow borders of basal 2–3 abdominal segments and midtibia light brown to yellowish. Genitalia dark brown to black laterally, brown to yellowish brown ventrally. Oral margin white.

Face and lower  $\frac{1}{2}$  of occiput gray pollinose with white pile and silvery scales, upper  $\frac{1}{2}$  of occiput black pollinose with mostly whitish pile, that along eye margin and immediately behind ocellus yellowish. Ocellar tubercle yellowish pilose, a few brownish hairs dorsoapically, 2nd antennal segment dark brown pilose. Front 0.3 mm, proboscis 2.9 mm, antennal ratio 2.4:1.0:5.6.

Scutum black pollinose dorsally with traces of brown; anterior margin, including corners and 2 admedian stripes gray; sides above wings brownish gray pollinose, postalar callus brown. Anterior  $\frac{1}{3}$  of scutum with scattered silvery to pale yellowish white scales and abundant white pile, posterior two-thirds with abundant golden scales and mostly shorter, less dense, dark brown to blackish pile, some longer yellowish pile posteriorly; sides above wings and postalar callus with scattered yellow hairs. Scutellum black pollinose with scattered golden scales and yellow pile. Pleuron mostly gray pollinose with silvery scales and white pile; anepimeron and meron bare. Halter yellowish white.

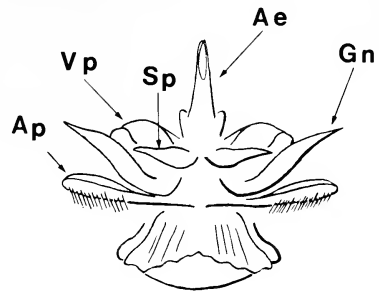
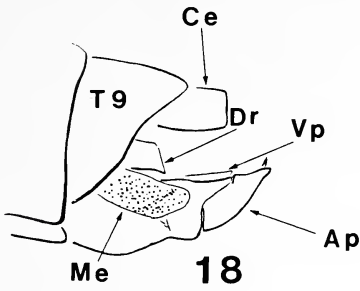
Coxae gray pollinose with white pile and silvery scales. Femora with mostly white scales and white pile, apical  $\frac{1}{3}$  to  $\frac{1}{2}$  of forefemur with pale brown scales; each femur with 2–3 brown hairs apically. Tibiae with blackish spines and mostly whitish scales.

Wing 3.9 mm, with subcostal cell pale yellow, cells otherwise hyaline. Veins generally brownish, slightly yellowish basally, node of M vein with a small black spot; r-m crossvein slightly beyond middle of discal cell, about same length as anal stalk; vein between discal and 1st medial cells slightly sinuous. Base of costal vein with yellow pile; squama and fringe white.

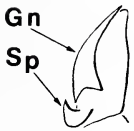
Abdomen blackish pollinose dorsally with whitish pile and yellow to golden yellow scales, apical 2–3 segments with scattered yellowish hairs; gray to brownish gray pollinose ventrally with white pile and silvery scales.

Genitalia (Figs. 18–20). Gonocoxite with whitish elliptical membrane basolaterally, apical process brownish pilose, subapically angular dorsally; dorsolateral ramus broadly joined in aedeagus, acutely angular apically. Gonostylus long, thick basally, slender

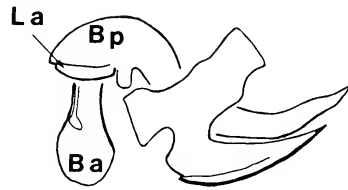




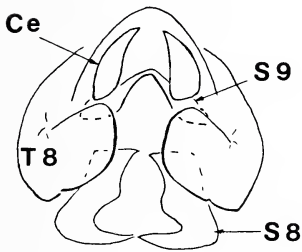
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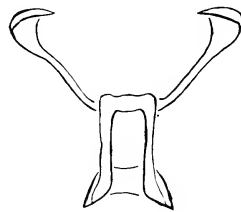
19b



20



21



22

Figs. 18–22. Genitalia of *G. exumae*; 18–20 male, 21, 22 female. 18. Closed condition, lateral view. 19a, Expanded condition, apical view; 19b, dorsal (above) and ventral (below) views of gonocoxite. 22. Vaginal apodeme.

apically. Vertical plate thick, with a strong basal spine. Aedeagus long, clearly exposed when genitalia are expanded, basal point rhomboid, lateral apodeme somewhat evenly rounded, basal apodeme slightly enlarged apically with a slender club-shaped thickening.

Female allotype. Differs from male as follows: length 4.0 mm, wing 3.9 mm, front 0.4 mm, proboscis 2.1 mm, antennal ratio 2.0:1.0:6.0. Oral margin yellowish white. Front mostly brownish pollinose with abundant golden scales and yellow to brownish yellow pile, silvery scales along eye margin below. Dorsal  $\frac{1}{2}$  of occiput, scutum, and tergites weakly brownish pollinose with abundant golden scales and yellow pile. Apical 3 tergites with scattered brownish hairs. Halter yellow.

Genitalia (Figs. 21, 22). Lobes of tergite 8 longer than wide, with 5–6 setae in a row. Sternite 8 rhomboid, weakly spinose apically, membrane bell-shaped. Dorsal arms of vaginal apodeme, flat, weakly capitate. Cercus apically truncate, with 2 alate plates basally.

Variation. Length  $\delta$  2.8 to 4.5 mm,  $\eta$  2.5 to 4.6 mm; wing  $\delta$  2.5 to 4.4 mm,  $\eta$  2.6 to 4.4 mm; proboscis  $\delta$  1.7 to 3.0 mm,  $\eta$  1.6 to 2.8 mm; front  $\delta$  and  $\eta$  0.2 to 0.3 mm; antennal ratio  $\delta$  2.0:1.0:6.0 to 3.3:1.0:6.6,  $\eta$  2.0:1.0:5.5 to 2.0:1.0:6.6. Oral margin usually creamy white although old or greased specimens are yellow. Basal antennal segment usually has slightly yellowish pile dorsally, with a few to several brownish hairs apically. One female has several yellow hairs on the 2nd antennal segment.

*Type material.* Holotype.  $\delta$ , Bahamas, Great Exuma Island, Simon Pt., 23.I.1982, T. McCabe. Allotype  $\eta$ , same data. Paratypes. 2 $\delta\delta$ , 2 $\eta\eta$ , 15–17.I.1982, same location and collector as types; Staniel Cay, Exuma, 3 $\delta\delta$ , 6 $\eta\eta$ , 25.IV.1981, C. A. Toft; Eleuthera Island, New Portsmouth, 3 $\delta\delta$ , 5 $\eta\eta$ , 28.III.1953, E. B. Haydes; Long Island, Deadman's Cay, 3.III.1953, E. B. Haydes; Cuba,  $\delta$  Soledad, ?VIII.?, Davenport; Soledad, Santa Clara Prov., 2 $\delta\delta$ , 4 $\eta\eta$ , 24–30.VI–VIII.1939, C. T. Brues; Same data, 4 $\delta\delta$ , 2 $\eta\eta$ , 20–25.II.1925.

The holotype and allotype are in the State Museum of New York, Albany. The paratypes are in the Albany Museum; Museum of Zoology, University of California, Davis; Museum of Comparative Zoology, Cambridge, Massachusetts; and the American Museum of Natural History, New York.

*Etymology.* This species is named after the Bahamian Island on which the fly was collected.

*Distribution.* Bahama Islands and Cuba. The seasonal distribution ranges from January through August.

### ***Geron binatus* Scarbrough, new species**

Figs. 23–25

*Diagnosis.* *Geron binatus* is recognized by its white oral margin, a large whitish triangle on the lower face; 1st antennal segment with mostly dark pile dorsally, 2nd antennal segment with black pile entirely, frontal pile yellow to brownish, apical 3 abdominal segments and cercus with abundant yellow and brownish black stiff hairs, apices of each femur with numerous brownish scales and several stiff brown hairs; gonocoxite deeply bilobed medially, each branch with 5 spatulate fingers; apical process of gonocoxite brown pilose, flattened dorsoventrally, and blade-like in outline

ventrally; vertical process and gonostylus fused, broad and thick basally, slightly longer than apical process; aedeagus almost straight, the apex concealed by an apically acute apodeme laterally.

*Geron binatus* is quite different from any other known *Geron* species in the Caribbean region, and is easily recognized by the characters of the head and details of the male genitalia.

*Description.* Male holotype. Length 6.3 mm. Ground color dark brown to black. Oral margin and large triangular area of lower face white. Tibia brown. Gonocoxite yellowish basally, shiny dark brown apically.

Face, front and lower  $\frac{1}{2}$  of upper occiput grayish pollinose with white pile and silvery scales, upper  $\frac{1}{2}$  of occiput blackish with pale yellow hairs, postocular pile and ocellar hairs blackish. Frontal pile yellowish to brownish, scales whitish to slightly yellowish. Second antennal segment with pile entirely black; 1st segment mostly dark pilose dorsally. Proboscis 3.0 mm, front 0.5 mm, antennal ratio 2.5:1.0:5.0.

Scutum and scutellum blackish pollinose with yellow to golden scales dorsally. Scutum weakly gray pollinose anteriorly, including 2 admedian stripes, with whitish pile; sides above wings, including postalar callus, brownish pollinose; posterior two-thirds of scutum with scattered brownish to blackish hairs, a few stiff hairs laterally and posteriorly. Scutellum yellow pilose. Pleuron grayish pollinose with white pile and silvery scales; anepimeron and meron bare.

Coxae grayish pollinose, with white scales and pile. Femora with mostly white scales and pile, apical  $\frac{1}{3}$  or more of each femur with brownish scales and several yellowish brown to brown hairs; tibiae with brownish and white scales intermixed; hindtibia with brownish scales more abundant.

Wing 4.1 mm, hyaline, subcostal cell slightly yellowish, veins slightly brownish, yellowish basally. R-m crossvein beyond middle of discal cell and slightly shorter than anal stalk; crossvein between discal and 1st medial cells sinuous. Pile of costa basally and fringe white, squamata white. Halter yellow.

Abdomen mostly black pollinose dorsally, with whitish pile and yellow scales, mostly grayish ventrally with whitish pile and silvery scales. Posterior 3 segments and cercus slightly brownish pollinose with abundant blackish brown and yellow hairs. Gonocoxite brownish pollinose with several stiff yellow hairs, deeply bilobed medially, apex of each branch with 5 small spatulate fingers.

Genitalia (Figs. 23–25). Gonocoxite with asymmetrical pyriform membrane basolaterally, apical process brown pilose, flattened dorsoventrally, apex narrowed, slightly curved laterally, blade-like in ventral view. Dorsal ramus narrowly connected to aedeagus, exposed below epandrium as a truncate plate. Gonostylus and vertical plate fused, thick basally, tapered apically, slightly longer than apical process. Aedeagus almost straight, basal point rounded, rhomboid-shaped; lateral apodeme slightly wider than long, basal apodeme rounded apically. Tip of aedeagus not noticeably exposed, concealed laterally by apically acute apodeme.

Female unknown.

*Type material.* Holotype. ♂, St. Johns, Antigua, 2–3.II.1965, H. E. Evans. The holotype is in the U.S. National Museum, Washington, D.C.

*Etymology.* The name *binatus* refers to the division of the gonocoxite into two branches.

***Geron declinatus* Scarbrough, new species**

Figs. 26–28

*Diagnosis.* *Geron declinatus* is recognized by its white oral margin, basal antennal segment entirely whitish pilose, 2nd segment black pilose, frontal pile and scales whitish, abdomen mostly white pilose, apical 3 segments and cercus with scattered yellow pile; male genitalia with apical process, gonostylus and vertical plate unusually slender and weak; aedeagus abruptly curved downward before basal point, apex not noticeably exposed when genitalia are expanded.

*Geron declinatus* is similar to *G. senilis* in that the basal antennal segment is entirely white pilose, which separates these species from the remaining Caribbean species. However, *G. declinatus* differs in that the 2nd antennal segment is wholly black pilose. The pile is entirely white on this segment in *G. senilis*.

*Description.* Male holotype. Length 5.1 mm. Ground color largely black. Oral margin white. Femora dark brown, tibiae brownish. Gonocoxite brownish basally, shiny dark brown apically.

Face, front and lower  $\frac{1}{2}$  of occiput grayish pollinose with white pile and silvery scales, upper  $\frac{1}{2}$  of occiput blackish pollinose with dull white pile; pile along eye margin slightly yellowish. Ocellar pile brown. Frontal pile white, scales mostly whitish, a few slightly yellowish. Second antennal segment wholly black pilose, 1st segment white pilose entirely. Proboscis length 2.3 mm, front 0.4 mm, antennal ratio 2.5:1.0:6.5.

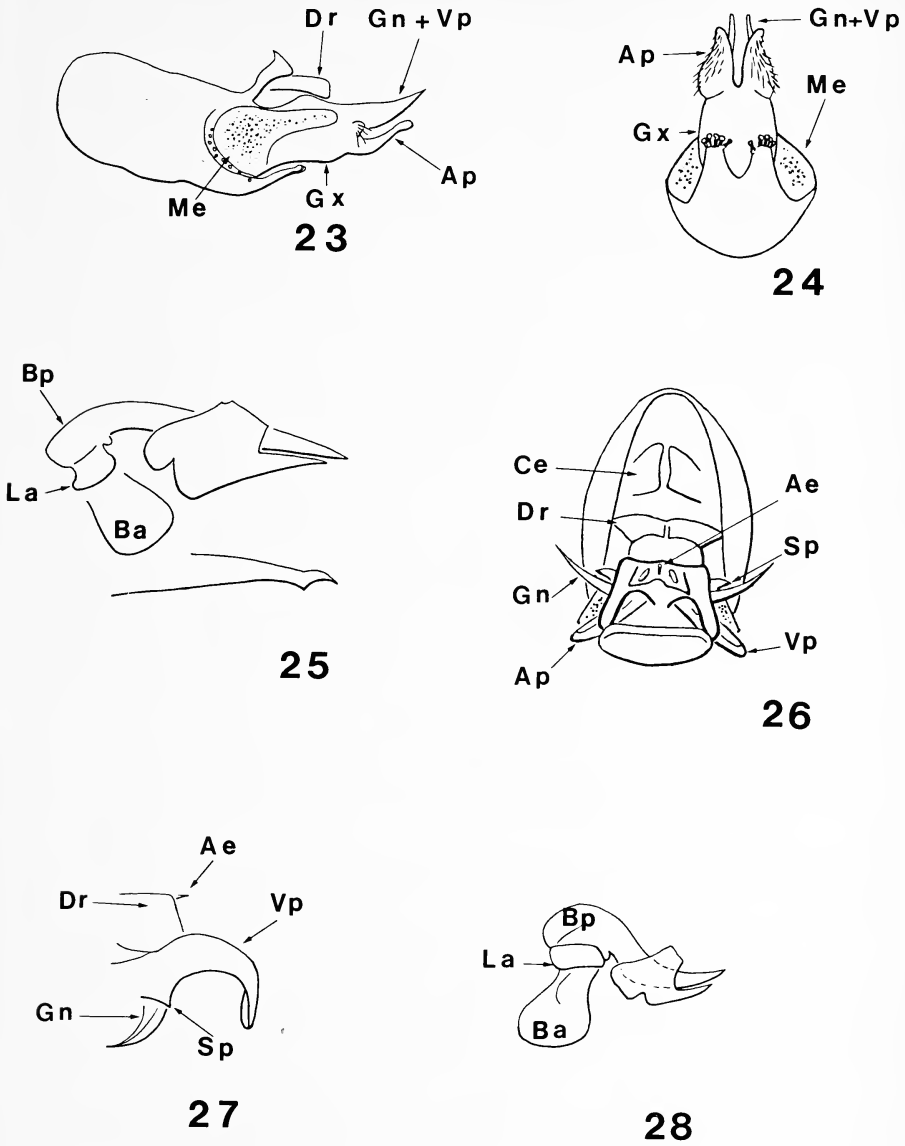
Scutum and scutellum mostly blackish pollinose with scattered yellow to golden scales. Scutum weakly gray pollinose anteriorly and laterally, including 2 admedian stripes. Pile whitish, dense anteriorly, posterior two-thirds of scutum with mostly scattered brownish to blackish pile, a few stiff yellow hairs laterally above wings, on postalar callus and along posterior margin. Scutellum yellow pilose. Pleuron grayish pollinose with white pile and silvery scales, anepimeron and meron bare.

Coxae grayish pollinose with white pile and scales. Femora with mostly white scales and pile, apical  $\frac{1}{3}$  of forefemur with pale yellowish or brownish scales. Tibiae with black spines, scales whitish.

Wing 5.2 mm, hyaline, subcostal cell weakly yellowish; vein slightly brownish apically, yellowish basally. R-m crossvein beyond middle of discal cell, slightly shorter than anal stalk; apical crossvein of discal cell slightly sinuous. Squama and fringe pile white. Costal vein with white pile basally. Halter creamy white.

Abdomen blackish pollinose dorsally with mostly white pile, apical 3 segments and cercus with scattered yellow pile, grayish pollinose ventrally with white pile and silvery scales.

Genitalia (Figs. 26–28). Gonocoxite linear with whitish basolateral membrane, apical process slender, about as long and wide as, or slightly larger than vertical plate, with brownish to yellowish pile. Dorsal ramus narrowly joined to aedeagus, anterior branch exposed as a folded plate (ca. 90°) below epandrium. Gonostylus and vertical plate unusually slender and weak, the former dagger-like, slightly shorter than apical process, plate decurved strongly when genitalia are expanded, with a weak basal spine. Aedeagus sharply curved downward before basal point, the latter rounded, rhomboid-shaped, lateral apodeme slightly wider than long. Apex of aedeagus short, not noticeably exposed when genitalia are expanded.



Figs. 23–28. 23–25. Male genitalia of *G. binatus*. 23. Closed condition, dissected, lateral view. 24. Closed condition, ventral view. 25. Lateral view of aedeagus (a) with an enlarged lateral apodeme (b) dissected. 26–28. Male genitalia of *G. declinatus*. 26. Expanded condition, apical view. 27. Gonostylus and vertical plate, expanded condition, lateral view. 28. Aedeagus, lateral view.



Female unknown.

*Type material.* Holotype. ♂, St. Johns, Antigua Island, 2-3.II.1965, H. E. Evans. The holotype is in the U.S. National Museum, Washington, D.C.

*Etymology.* The name *declinatus* refers to the strongly decurved shape of the vertical plate when the genitalia are expanded.

***Geron articulatus* Scarbrough, new species**

Figs. 29-31

*Diagnosis.* *Geron articulatus* is recognized by its whitish oral margin, basal antennal segment with mostly whitish pile, mostly brownish pile dorsally, 2nd antennal segment brown pilose, frontal pile and scales white, abdominal tergites yellowish pilose dorsally, apical ½ of hindfemur with numerous brown hairs, gonostylus short and articulated near apex of vertical plate; vertical plate short with basal spine small.

*Geron articulatus* is similar to *G. exumae*, new species in general appearance but is readily recognized by the usual abundant dark pile on the basal antennal segment dorsally and by the detailed characters of the male genitalia.

*Description.* Male holotype. Length 5.3 mm, ground color largely dark brown to black, oral margin whitish, femora dark brown, tibiae and sides of 1st tergite yellowish brown.

Face, front and lower ½ of occiput grayish pollinose with whitish pile and silvery scales, upper ½ of occiput slightly brownish black pollinose with dull white pile. Ocellar tubercle with brownish pile, pale yellowish scales scattered posteriorly. Antenna with 2nd segment brown pilose, basal segment mostly whitish pilose, brownish dorsally. Antennal ratio 2.4:1.0:?, proboscis 2.9 mm, front 0.4 mm at antennal base.

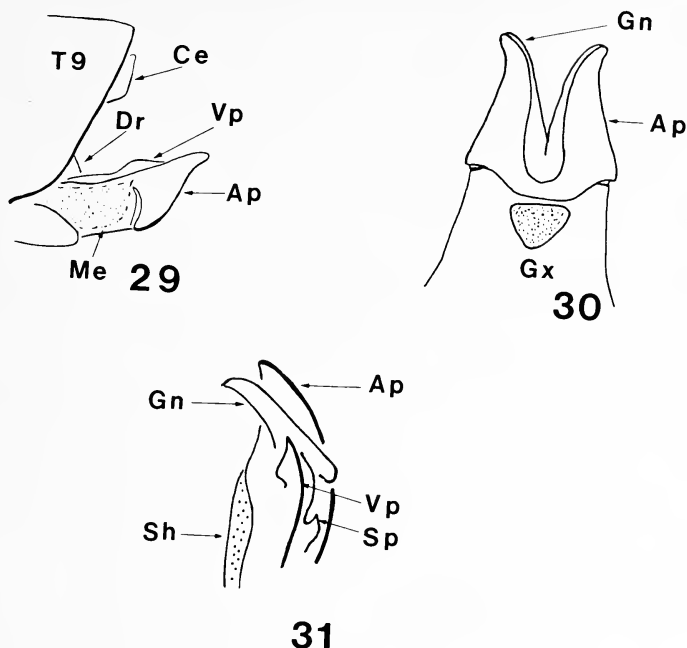
Scutum mostly and scutellum entirely brownish black pollinose, anterior margin of scutum including 2 admedian stripes and entire pleuron grayish. Scutum with mostly scattered blackish brown pile and golden scales; pile yellowish laterally and posteriorly, anterior margin with whitish pile and scattered whitish scales. Scutellum with yellow pile and golden scales. Pleuron with silvery scales and white pile; meron and anepimeron bare. Halter creamy white.

Coxae gray pollinose with white pile and silvery scales. Femora with whitish scales and whitish pile, apical ¼ or more of each femur with brown scales dorsally, apical ½ of hindfemur with numerous brown hairs. Tibiae with mostly white scales dorsally, hindtibia with brown and white scales mixed dorsally. Tibial spines brownish.

Wing 5.1 mm, hyaline, subcostal cell yellowish. Veins yellowish to yellowish brown, node of vein M with dark spot, vein between discal and 1st medial cells sinuous. Anal stalk slightly shorter than r-m crossvein, the latter beyond middle of discal cell. Costal vein with yellow pile basally, squama yellowish, fringe white.

Abdomen brownish black pollinose dorsally with golden scales and yellow pile gray pollinose ventrally with white pile and silvery scales.

Genitalia (Figs. 29-31). Gonocoxite elongate, basolateral membrane brownish, a small oval or triangular whitish membrane medioventrally; apical process somewhat triangular in lateral view with brown pile; dorsolateral ramus broadly connected to aedeagus. Vertical plate somewhat short, with brown membranous depression medially and a small spine basally. Gonostylus shorter than apical process, strong,



Figs. 29–31. Male genitalia of *G. articulatus*. 29. Closed condition, lateral view. 30. Closed condition, ventral view. 31. Dorsal view showing apical process, gonostylus and vertical plate, dissected.

slightly tapered unilaterally, articulated near apex of vertical plate. Aedeagus slender, slightly undulate, basal point rhomboid, lateral apodeme length twice its width.

Female unknown.

*Type material.* Holotype. ♂, Palo Verde Monte Cristy en fin cadela Nebrasco, 4.III.1967, Todo en Sorgo, Marciano F. The holotype is in the U.S. National Museum, Washington, D.C.

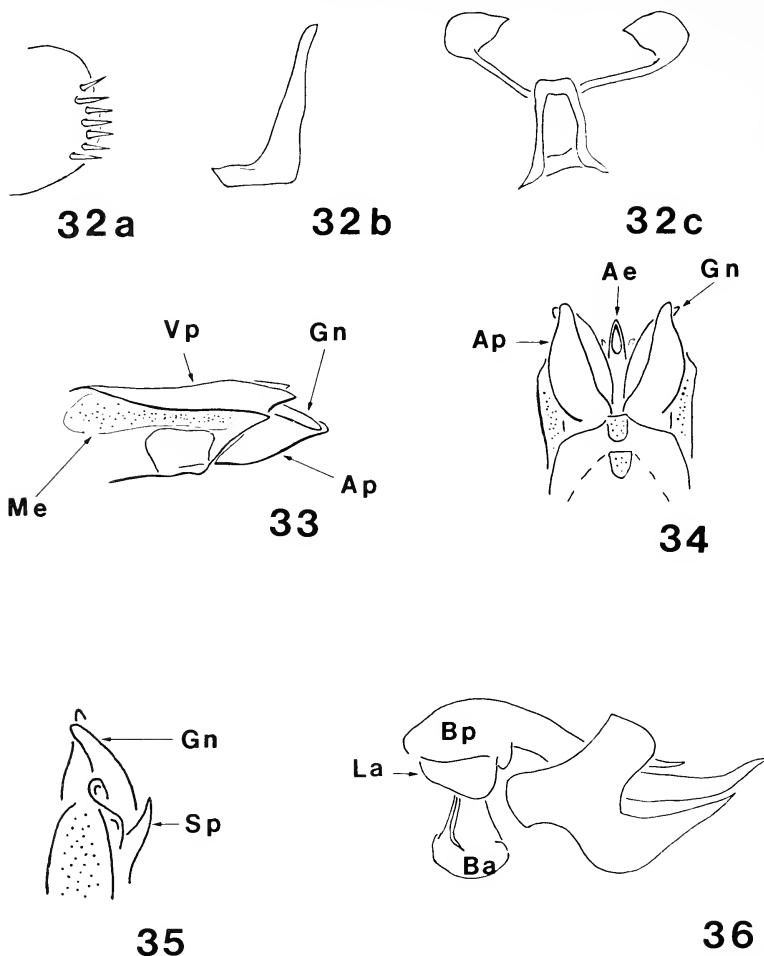
*Etymology.* The name *articulatus* refers to the union of the gonostylus with the genitalia.

### ***Geron nephroideus* Scarbrough, new species**

Figs. 32–36

*Diagnosis.* *Geron nephroideus* is recognized by its yellowish oral margin; basal antennal segment with yellowish to yellowish white pile dorsally, white ventrally; costal vein with basal pile white; veins of wing yellowish; male with dull white occipital, thoracic and abdominal pile, unusually long and dense on entire thoracic dorsum; aedeagus length subequal to apical process; female with dorsal arms of vaginal apodeme strongly capitate or kidney-shaped apically.

*Geron nephroideus* is similar to *G. exumae*, new species and *G. salmonus*, new



Figs. 32–36. Genitalia of *G. nephroideus*; 32 female, 33–36 male. 32. Lobe of tergite 8 (a), sternite 9 (b) and vaginal apodeme (c). 33. Closed condition, lateral view, tergite 9 and cercus removed. 34. Closed condition, ventral view. 35. Gonocoxite and gonostylus, dorsal view. 36. Aedeagus.

species but is easily separated from these species by the characters listed in the diagnosis.

*Description.* Female holotype. Length 6.6 mm. Ground color generally blackish, oral margin yellowish, femora dark brown, foretibia brown, mid- and hindtibiae yellowish brown.

Head generally gray pollinose, upper  $\frac{1}{2}$  of occiput blackish. Face and lower  $\frac{1}{2}$  of occiput with white pile and silvery scales, front with abundant golden scales and yellow pile, silvery scales along eye margin and just above antenna. Dorsal  $\frac{1}{2}$  of

occiput with abundant golden scales and yellow pile. Ocellus yellow pilose. Basal antennal segment with yellowish pile dorsally, white ventrally, 2nd segment yellowish and white intermixed dorsally, pale yellow to white ventrally. Front 0.5 mm at antennal base, proboscis 3.6 mm, antennal ratio 2.8:1.0:6.8.

Scutum mostly and scutellum entirely blackish pollinose with yellow scales and mostly yellowish pile, scattered brownish black pile on posterior two-thirds. Scutum anteriorly, including 2 admedian stripes, and pleuron grayish, the latter white pilose with silvery scales; anepimeron and meron bare.

Legs mostly white pilose with white scales, anterior  $\frac{1}{3}$  to  $\frac{1}{2}$  of forefemur with brownish scales. Tibiae with brown spines.

Wing 6.1 mm, hyaline, veins yellowish, r-m crossvein beyond middle of discal cell, slightly longer than anal stalk; crossvein between discal and 1st medial cells strongly sinuous. Squama and fringe white. Costal vein with basal pile whitish.

Abdomen brownish black pollinose dorsally with yellowish pile and scales, gray pollinose ventrally with white pile and silvery scales.

Genitalia (Fig. 32). Tergite 8 with lobes longer than wide and a subapical row of 7–8 strong setae on inner margin. Cercus subtruncate, with a pair of long, slender plates, basal width less than length. Sternite 8 typically rhomboid, weakly spinose apically, with bell-shaped membrane. Vaginal apodeme with dorsal arms slender, abruptly enlarged apically, strongly bean- or kidney-shaped.

Male allotype. Differs from female as follows: length 7.6 mm, front 0.5 mm, proboscis 3.0 mm, wing 6.9 mm, antennal ratio 2.4:1.0:7.0. Pile generally dull white, slightly longer than usual and unusually dense, especially on posterior two-thirds of scutum. Basal antennal segment yellowish white to white entirely, 2nd antennal segment with mostly yellowish white pile, scattered yellowish brown pile dorsally. Scales of scutum and abdomen whitish.

Genitalia (Figs. 33–36). Gonocoxite with elongate basolateral membrane, apical process yellowish pilose, inner margin slightly flared subapically and curved below gonostylus; vertical plate prominent, apically pointed and with a strong basal spine. Dorsolateral ramus of gonocoxite broadly joined to aedeagus. Aedeagus long, length subequal to apical process when genitalia are closed; basal point suboval, basal apodeme club-shaped apically, lateral apodeme alate.

*Type material.* Holotype. ♀, Cuba, Poey on green label, date ?, Loew. Allotype, ♂ (damaged), same data. Both specimens are in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

*Etymology.* The name *nephriodeus* refers to the bean- or kidney-shape of the dorsal arms of the vaginal apodeme in the female.

#### ACKNOWLEDGMENTS

We thank Jack C. Hall, Department of Entomology, Division of Biological Control, University of California; Neal L. Evenhuis, Department of Entomology, Bishop Museum, Honolulu, Hawaii; and George S. Steyskal, Systematic Entomology Laboratory, ARS, USDA, Washington, D.C., for their helpful suggestions and critical reviews of the manuscript; Lloyd V. Knutson and Raymond Gagné of the Systematic Research Laboratory, ARS, USDA, Washington, D.C., for many helpful suggestions and providing working space and access to the collections of the United States National Museum; Loïc Matile, Muséum National D'Histoire Naturelle, Paris,

France and Leif Lyneborg, Universitetets Zoologiske Museum, Copenhagen, Denmark, are acknowledged for the loan of type specimens. Catherine A. Toft, Department of Zoology, University of California, Davis; Norman E. Woodley and Karen Jepson, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; and several Towson State University students contributed specimens to the study. We also thank Donald Gerace, Director of the College Center of the Finger Lake School, Marine Research Laboratory, San Salvador Island, the Bahamas, for providing transportation and working facilities, and the Faculty Research Committee of Towson State University for support of this research.

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NEW FAMILY PLACEMENT FOR THE GENUS *CYNIPENCYRTUS*  
(HYMENOPTERA: CHALCIDOIDEA: TANAOSTIGMATIDAE)

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*Abstract.*—The genus *Cynipencyrtus* is moved to the Tanaostigmatidae from the Encyrtidae. Characters are given to distinguish this genus from Encyrtidae, and from other Tanaostigmatidae. A redescription of the genus is given.

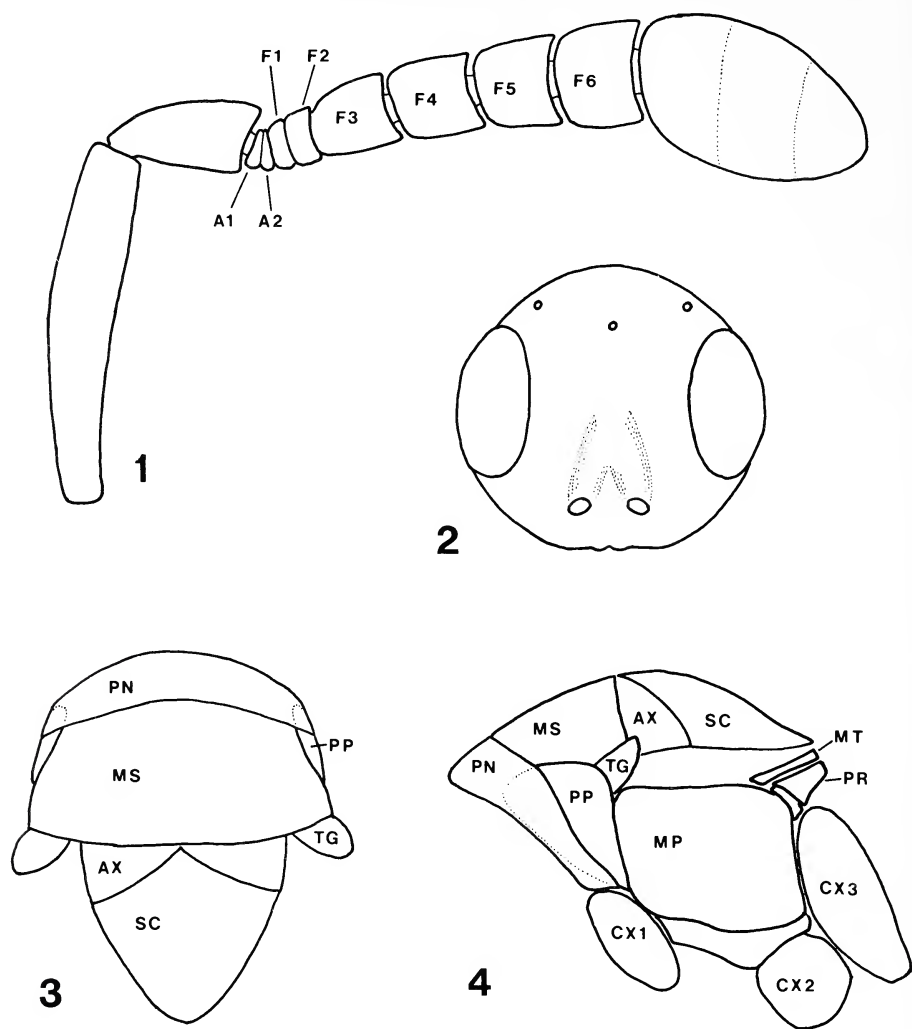
*Cynipencyrtus* Ishii was originally placed in the Encyrtidae. Subsequent workers maintained this placement, although Compere and Annecke (1960) and Tachikawa (1963, 1978) noted that this genus is so distinct morphologically as to be difficult to place satisfactorily within this family. Our examination of the genus reveals that it does not belong in the Encyrtidae, but in the closely related family Tanaostigmatidae.

Tanaostigmatids are distinguished from encyrtids and other chalcidoids by a single apomorphy, the presence of a large prepectus which is distinctly swollen anteriorly. Not only does *Cynipencyrtus* possess this attribute, it also lacks several apomorphic character states which are found in encyrtids. These differences between encyrtids and tanaostigmatids are given in Table 1. Although *Cynipencyrtus* belongs in the Tanaostigmatidae, it is distinct from other members of this family, and is distinguished by several unique character states which are given in Table 2.

The antenna of *Cynipencyrtus* was previously described as having 2 anelli and 5 funicular segments (Ishii, 1928), or 3 anelli and 4 funicular segments (Tachikawa, 1963). There are actually 2 anelli (which are very small, and difficult to distinguish

Table 1. Differences between Tanaostigmatidae and Encyrtidae. Apomorphic character states are marked by an asterisk.

Encyrtidae	Tanaostigmatidae
Prepectus not swollen	*Prepectus, large, distinctly swollen anteriorly
*Cerci usually advanced on metasoma	Cerci situated at apex of metasoma
*Articulation of middle coxa usually anterior to midline of mesosternum	Articulation of middle coxa posterior to midline of mesosternum
*Marginal vein usually very short, often punctiform or wider than long, rarely as long as stigmal vein	Marginal vein distinctly longer than wide (more than 5 times); longer than stigmal vein
*Antenna at most with 1 anellus and with from 2 to 7 funicular segments	Antenna with 2 anelli and 6 funicular segments



Figs. 1-4. *Cynipencyrtus flavus* Ishii, female. 1. Antenna. 2. Head, frontal view. 3. Mesosoma, dorsal view, showing only pronotum, mesoscutum, prepectus, tegula, scutellum, axilla. 4. Mesosoma, lateral view. A, anellus; AX, axilla; CX, coxa; F, funicular segment; MP, mesopleuron; MS, mesoscutum; MT, metanotum; PN, pronotum; PP, prepectus; PR, propodeum; SC, scutellum; TG, tegula.

even with good preparation and optics) and 6 funicular segments, the first 2 of which are reduced in size to only slightly larger than anelli (Fig. 1).

Biologically, *Cynipencyrtus* differs from other tanaostigmatids in host preference. Individuals are entomophagous, being parasitic on several species of Cynipidae that

Table 2. Differences between *Cynipencyrtus* and other genera of the Tanaostigmatidae.

<i>Cynipencyrtus</i>	Other Tanaostigmatidae
First 2 funicular segments reduced to the size of anelli (Fig. 1)	Rarely with first funicular segment reduced to the size of an anellus, usually with no segments so reduced
Pronotum clearly visible in dorsal view; partially overlapping prepectus laterally (Figs. 3, 4)	Pronotum not or only barely visible in dorsal view; not overlapping prepectus
Notauli absent (Fig. 3)	Notauli present, usually complete
Vertex vaulted, projecting distinctly above dorsal eye margin (Fig. 2)	Vertex not vaulted, not or only slightly projecting above dorsal eye margin
Ocelli small and widely separated, distance between lateral ocellus and median ocellus more than 5 times diameter of ocellus (Fig. 2)	Ocelli not small and not widely separated, distance between lateral ocellus and median ocellus usually less than twice diameter of ocellus

form galls on *Quercus serrata* (Ishii, 1928; Tachikawa, 1973, 1978). All other tanaostigmatids are phytophagous, the majority being gall-formers.

*Cynipencyrtus* Ishii

*Cynipencyrtus* Ishii, 1928:102, 106–107. Type species *Cynipencyrtus flavus* Ishii, 1928 (original designation).

*Cynipencyrtus* was described with two included species: *C. flavus* and *C. bicolor* Ishii (1928). These two species were later synonymized (Tachikawa, 1978), and the genus presently contains only the single species, *C. flavus*.

Female: *Head* (Fig. 2) vaulted between eyes, vertex in frontal view distinctly higher than dorsal margin of eye. Occipital margin narrowly rounded. Ocelli small, widely separated; lateral ocellus separated from eye margin by twice its own diameter, and from median ocellus by at least 5 times its own diameter. Antenna inserted low on face, below level of ventral margin of eye. Mandible with three teeth.

*Antenna* (Fig. 1) with two anelli and 6 funicular segments. Anelli very small and hard to differentiate from each other. First 2 funicular segments much smaller than following segments, only slightly larger than the anelli. Scape elongate. Club entire, with two very weak transverse sutures.

*Mesosoma* (Figs. 3, 4) with transverse pronotum clearly visible in dorsal view; in lateral view posterior margin of pronotum overhanging and partially obscuring prepectus. Mesoscutum without notauli. Prepectus large, swollen anteriorly, partially obscured anteriorly by pronotum, broadly attached posteriorly to the mesopleuron. Middle coxa inserted near the posterior margin of the mesopleuron.

*Wings* hyaline. Fore wing with marginal vein slightly longer than stigmal vein. Postmarginal vein distinctly longer than marginal vein.

*Metasoma* with posterior margin of all terga straight, without medial incision. Cerci located apically on the metasoma.

Male: Similar to female except in genitalia. Antenna displaying no sexual dimorphism.

#### ACKNOWLEDGMENTS

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## ON THE MONOPHYLY OF THE SPIDER SUBORDER MESOTHELAE (ARACHNIDA: ARANEAE)

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**Abstract.**—A newly observed character, apparently unique to liphistiid spiders, supports a hypothesis of their monophyly. Flattened spurs situated distally on the prolateral and retrolateral sides of tibiae I-III can contact slightly raised, oval, unsclerotized areas situated proximally on the sides of metatarsi I-III. The character is found in juvenile and adult females and in juvenile males, and may function as a proprioceptor of lateral leg deflection.

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Liphistiids have long been regarded as the most primitive of living spiders, primarily because of their retention of such obviously plesiomorphic features as a full complement of abdominal tergites and two pairs of booklungs. As indicated by Haupt (1983), hypotheses of monophyly are particularly crucial for groups that (like the Mesothelae) were classically recognized largely or entirely on the basis of plesiomorphies. Platnick and Gertsch (1976) examined the Mesothelae and concluded, on the basis of four putative synapomorphies, that the groups is indeed monophyletic. Haupt (1983, fig. 15) accepted this conclusion and used those four synapomorphies at the base of a cladogram of the three genera he recognized within the group.

Haupt (1983, p. 289) also put forward, however, a list of conceivable objections to those four putative synapomorphies. For example, with regard to Platnick and Gertsch's first character (invaginated fourth coxae), Haupt conjectured that those invaginations might be functionally correlated with the (plesiomorphic) retention of the first opisthosomal sternite, and hence might also be plesiomorphic. But the relevant outgroup (the Amblypygi) belies that conjecture, for at least some amblypygids do retain the first abdominal sternite (often in a bipartite form), but nonetheless lack invaginations on the fourth coxae. Rather than respond in similar fashion to Haupt's other conceivable objections (which even he ultimately disregarded in his cladogram), we present instead new evidence relevant to the hypothesis. This consists

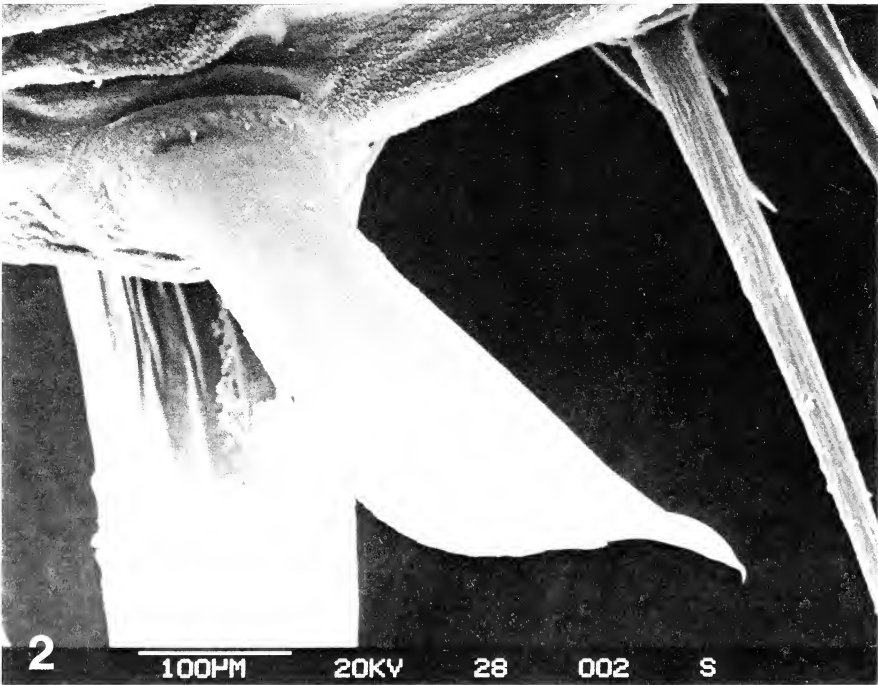
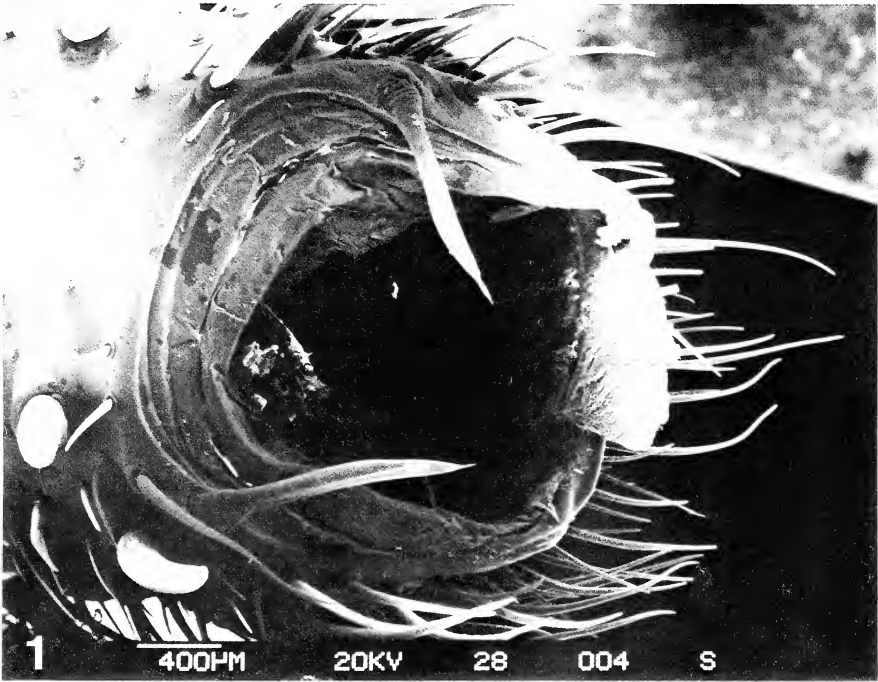
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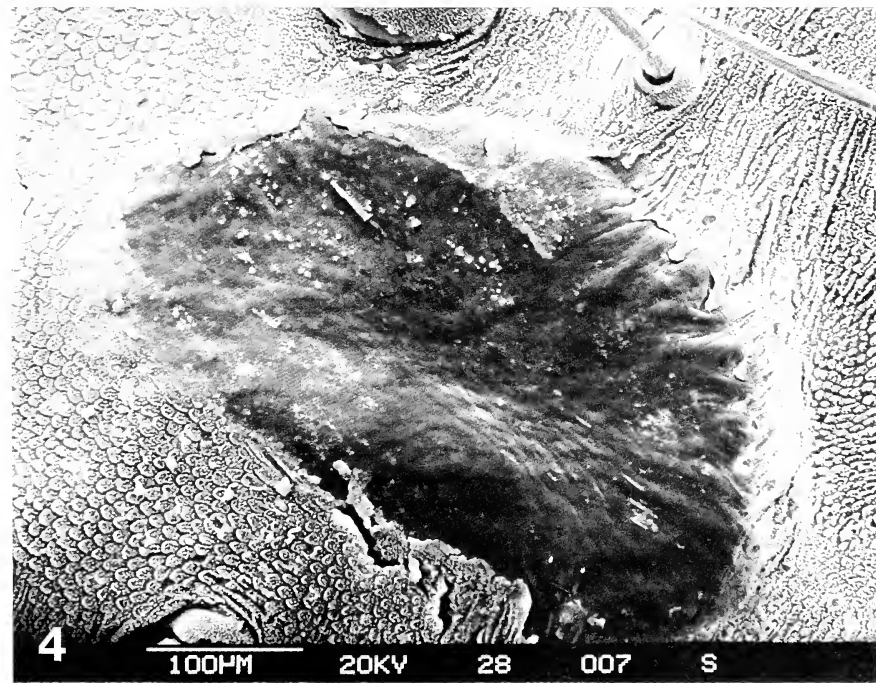
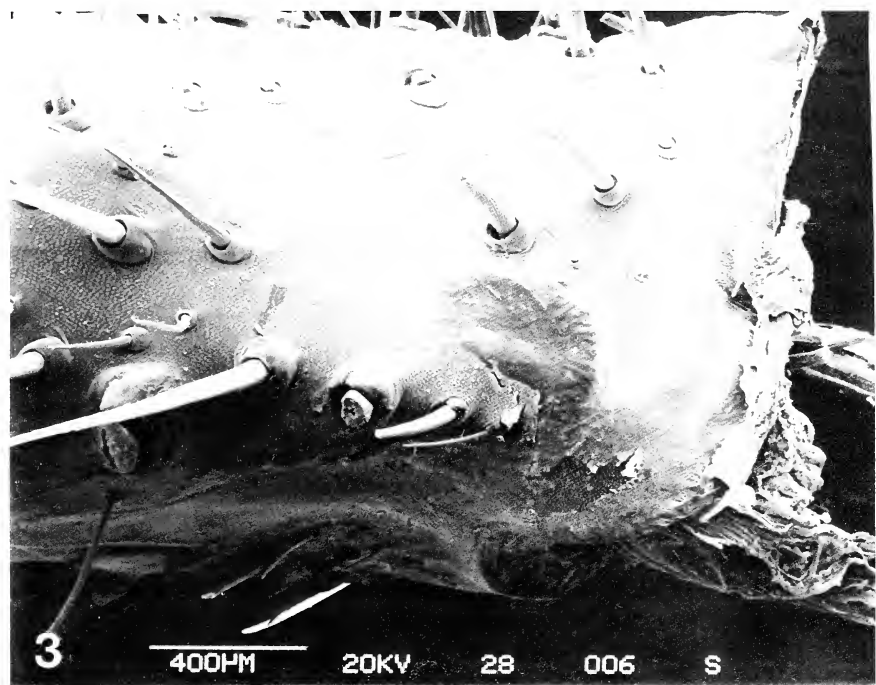
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Figs. 1, 2. Tibial spurs from leg I of a female of *Liphistius malayanus* Abraham. 1. Distal view of tibia, with metatarsus and tarsus removed and ventral surface at left. 2. Inner surface of a tibial spur.

Figs. 3, 4. Metatarsal unsclerotized area from leg I of a female of *Liphistius malayanus* Abraham. 3. Metatarsus, showing location of unsclerotized area. 4. Unsclerotized area; note lack of denticulate sculpturing.







of a character, apparently overlooked in previous work on liphistiids, that seems to be unique to them and therefore to offer strong support for their monophyly.

The character consists of a pair of wide, flattened spurs situated distally on the prolateral and retrolateral sides of tibiae I, II, and III (Figs. 1, 2); the tips of those spurs override slightly raised, oval, unsclerotized areas situated proximally on the prolateral and retrolateral surfaces of metatarsi I, II, and III (Figs. 3, 4). The tibial spurs are readily distinguished from the normal leg setae and spines by their shape and unarticulated bases; the unsclerotized metatarsal areas lack the denticulate sculpturing characteristic of the remainder of the liphistiid leg cuticle.

The tibial spurs have been observed in both juvenile and adult females; they occur in penultimate males but are lost in adults of that sex, suggesting that they do not play a stridulatory role in mating (scanning electron micrographs also reveal no rasping structures on either the inner surface of the tibial spurs or on the unsclerotized metatarsal areas). The spurs are so situated, however, that even a slight lateral deflection of the metatarsus relative to the longitudinal axis of the tibia presses one or the other spur against a metatarsal area. It seems likely, therefore, that the structures function as proprioceptors of lateral leg deflection.

The character was first observed (by the second author) in a female of *Liphistius malayanus* Abraham, and we have subsequently been able to confirm its presence in *L. birmanicus* Thorell, *L. lordae* Platnick and Sedgwick, *L. bristowei* Platnick and Sedgwick,<sup>1</sup> *L. yangae* Platnick and Sedgwick, *L. langkawi* Platnick and Sedgwick, *L. murphyorum* Platnick and Sedgwick,<sup>1</sup> *L. desultor* Schiödt, *L. sumatranus* Tho-

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<sup>1</sup> Unfortunately, two specific names, *Liphistius bristowei* and *L. murphyorum*, have been validated twice in recent papers by Haupt (1983) and by Platnick and Sedgwick (1984). Although the issue (December 1983) of the journal including Haupt's paper bears no specific publication date, his usage of those names apparently has priority, for that issue was received by the Library of the American Museum of Natural History on February 4, 1984, four days before the Platnick and Sedgwick paper was published. Nonetheless, the authorship of the two names should not be attributed to Haupt.

Upon completion of their *Liphistius* revision, Platnick and Sedgwick sent a copy of their manuscript to Haupt, for they proposed a relimitation of the genus vis-à-vis *Heptathela* and Haupt had worked extensively with that genus (as it happened, those authors and Haupt had independently reached the same conclusion regarding the generic limits). Haupt was kind enough to send several helpful comments on the manuscript, perhaps the most useful of which indicated that the Zoologisk Museum, Copenhagen, housed a male *Liphistius* from the type locality of a species Platnick and Sedgwick were describing as new on the basis of females only (*L. bristowei*). Thanks to the prompt assistance of Dr. H. Enghoff of that institution, Platnick and Sedgwick were able to borrow the male specimen in time to include it in their published paper as the holotype of *L. bristowei*.

From the Platnick and Sedgwick manuscript, Haupt determined that he had misidentified two specimens in his paper, then already in proofs. One was the male just mentioned, which Haupt had erroneously placed as the male of *L. birmanicus* Thorell. The other was a male from Penang Island, Malaysia, belonging to *L. murphyorum*; like Murphy and Platnick (1981), Haupt had misidentified a male of this small species as that of the much larger *L. desultor* Schiödt. Haupt sent Platnick and Sedgwick a copy of his proofs, indicating that he was correcting these two misidentifications and listing the specimens as merely "n. sp. A" and "n. sp. B." In the published version, both headings include descriptions and references to illustra-



rell, *L. batuensis* Abraham, *L. panching* Platnick and Sedgwick, and *L. tioman* Platnick and Sedgwick. In view of the loss of the tibial spurs in adult males (which abandon their burrows to search for females) and their absence from the fourth legs (which, unlike legs I–III, are generally not used by *Liphistius* to monitor the “fishing lines” of silk radiating from the burrow entrance; see Platnick and Sedgwick, 1984, figs. 4, 5), it is tempting to associate the character with the use of “fishing lines.” However, the tibial spurs also occur in *Heptathela kimurai* Kishida, *H. sinensis* Bishop and Crosby, *H. schensiensis* (Schenkel), *H. bristowei* Gertsch, and “*Ryuthela*” *nishihirai* (Haupt),<sup>2</sup> which (so far as is known) construct burrows without “fishing lines.” Moreover, the fourth metatarsi of females and juvenile males, and all the metatarsi of adult males, occasionally show what appear to be remnants of the unsclerotized areas, even though the tibial spurs are absent.

Both the tibial spurs and metatarsal unsclerotized areas seem to be unique to the Mesothelae. We are unaware of similar structures in any other group of spiders, and a search for possible homologs in amblypygids and in the more plesiomorphic families of mygalomorphs (Atypidae, Antrodiaetidae, Mecicobothriidae, Microstigmatidae, and Hexathelidae) has been unsuccessful. We therefore regard the structures as a fifth synapomorphy of the suborder.

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tions that would be sufficient to validate names had any been given there; “n. sp. A” is given only a “Locus typicus” but under “n. sp. B” a holotype is designated (although, of course, only a specific name can actually have a holotype).

No nomenclatorial difficulties arise from this portion of Haupt’s treatment. However, Haupt had indicated that he also planned to add a final note to his proofs saying that “n. sp. A” and “n. sp. B” would be described as *L. murphyorum* and *L. bristowei*, respectively, in the Platnick and Sedgwick revision. Those authors immediately (September 20, 1983) requested that he *not* add such a note, and repeated that request in another letter of December 2, 1983. Despite their informing Haupt on both occasions that the addition of such a note, in conjunction with his brief treatments of “n. sp. A” and “n. sp. B,” would be sufficient to validate the names, the published version of Haupt’s paper does include the final note (p. 293). That note makes it clear, however, that Platnick and Sedgwick are alone responsible for the names, and Haupt has informed us that he intends to request the International Commission of Zoological Nomenclature to suppress his usage of the two names. Accordingly, we here attribute the names to their legitimate authors.

<sup>2</sup> Raven (in press) rejects Haupt’s proposal of a separate genus for this species and hence also Haupt’s proposal of a separate family Heptathelidae.

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## **PHYTCORIS ADENOSTOMAE, A NEW MIRINE PLANT BUG (HETEROPTERA: MIRIDAE) FROM SOUTHERN CALIFORNIA**

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**Abstract.**—The new plant bug *Phytocoris adenostomae* is described from southern California where it breeds on *Adenostoma sparsifolium* Torr. (Rosaceae). The male genitalic structures are figured, and a photograph of the adult male and scanning electron micrograph of the dorsal vestiture are provided.

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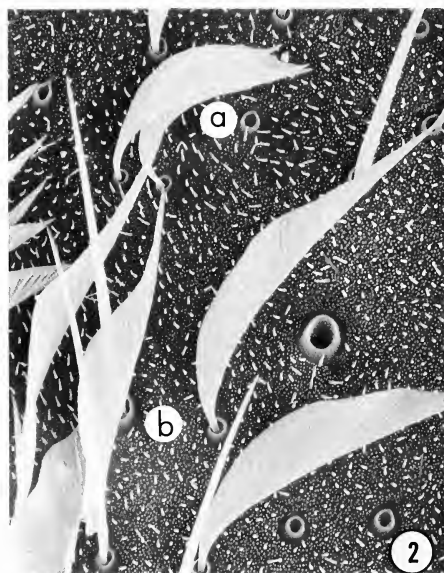
The genus *Phytocoris* contains 162 species from western America north of Mexico (Stonedahl, 1983). A manuscript in preparation by the author will include an additional 30 new species in a revisionary study of *Phytocoris* for that region. *Phytocoris adenostomae* is described here to validate the name for use in a study of Miridae associated with *Adenostoma* in California (conducted by John D. Pinto, Department of Entomology, University of California, Riverside, California 92521).

### ***Phytocoris adenostomae*, new species**

Figs. 1-7

**Diagnosis.** Distinguished from other species of *Phytocoris* in western North America by its small size, 3.94-4.48 mm; yellowish red general coloration, with fuscous markings on outer half of clavus and inner apical region of corium; dorsal vestiture with both silvery white and black, scale-like setae intermixed with dark simple setae (Fig. 2); short first antennal segment with erect, black bristle-like setae dorsally; and by the structure of the male genitalia, particularly the broad, densely setose tubercle on the genital capsule above the base of the left paramere (Fig. 3).

**Description.** Male. Length 3.94-4.48 (all measurements in millimeters), width 1.26-1.57; yellowish red general coloration with limited reddish brown or fuscous markings. Head: width across eyes 0.75-0.84, vertex 0.33-0.36; yellow or grayish yellow with red markings; frons moderately convex, meeting tylus along broad depression; eyes large, occupying slightly more than two-thirds head height; lower margin of antennal fossa situated slightly above ventral margin of eye. Rostrum: length 1.57-1.75, extending to 4th or 5th abdominal segment. Antennae: I, length of 0.57-0.67, red or reddish brown with white spots and 8-12 erect black bristle-like setae dorsally; II, length 1.40-1.57, brownish yellow, sometimes slightly darker apically; III, length 0.91-1.04, brown or fuscous, narrowly pale basally; IV, length 0.64-0.72, brown or fuscous. Pronotum: mesal length 0.59-0.75, posterior width 1.06-1.31; pronotal disk yellow or grayish yellow with red or reddish brown tinge; collar and calli sometimes extensively reddened; posterior submargin of disk with several weakly elevated, sometimes faintly infuscated, points; propleura pale brownish yellow, sometimes with scattered red markings and brownish tinge. Scutellum: weakly convex; yellow

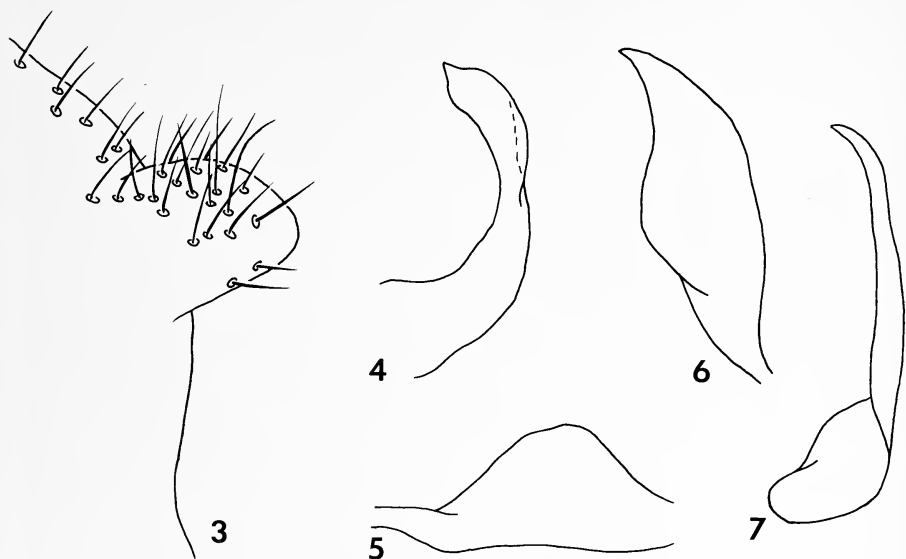


Figs. 1–2. *Phytocoris adenostomae*. 1. Adult female, dorsal view. 2. Dorsal vestiture: a, white scale-like setae; b, black scale-like setae.

or brownish yellow with red markings. Hemelytra: pale yellow or grayish yellow, moderately to extensively tinged or marked with red; outer half of clavus, inner apical region of corium, and inner margin and apex of cuneus usually marked with brown or fuscous; membrane extensively darkened, sometimes almost entirely fuscous with limited pale spots, veins infuscated except reddish distally. Venter: brownish yellow, moderately to extensively darkened with red or deep reddish brown. Legs: femora pale brownish yellow with red or reddish brown reticulations mostly on distal half of segment; hind femora more extensively darkened distally and marked with pale spots; tibiae red or reddish brown with pale spots. Vestiture: dorsum with dark simple setae intermixed with lanceolate flattened black setae and silvery white scale-like setae with apical serrations (Fig. 2). Genitalia: Figures 3–7. Genital capsule with broad, densely setose tubercle above base of left paramere (Fig. 3).

Female (Fig. 1). Similar to male in color, structure, and vestiture. Length 3.94–4.48, width 1.31–1.53. Head: width across eyes 0.76–0.81, vertex 0.37–0.40. Rostrum: length 1.66–1.84, extending to 5th or 6th abdominal segment. Antennae: I, 0.59–0.72; II, 1.46–1.67; III, 0.95–1.08; IV, 0.61–0.74. Pronotum: mesal length 0.61–0.72, posterior width 1.15–1.33.

*Type data.* Holotype: ♂, Oak Grove, San Diego Co., California, September 10, 1975, ex *Adenostoma sparsifolium* Torr., J. D. Pinto (AMNH). Paratypes: CALIFORNIA. Riverside Co.: 6♂♂, 4♀♀, same data as holotype (UCR); Palm Cyn., ca. 5 mi S Palm Springs, collected at light: 3♂♂, 5♀♀, July 1978, J. D. Pinto (UCR); 2♂♂, 3♀♀, September 29, 1978, K. Cooper (UCR).



Figs. 3–7. *Phytocoris adenostomae*, male genitalia. 3. Tubercle on genital capsule above base of left paramere, lateral view. 4. Apex of left paramere, dorsal view. 5. Base of left paramere, lateral view. 6. Right paramere, lateral view. 7. Sclerotized process of vesica, lateral view.

*Additional specimens.* 98 specimens were examined from the following localities: CALIFORNIA. Los Angeles Co.: Mint Cyn. (KU). Riverside Co.: Andreas Cyn. (UCR); Anza (KU); 3 mi E Anza (UCR); Deep Cyn. (UCR); Idyllwild (KU); 5 mi S Palm Spgs. (UCR); San Jacinto Mts., Herkey Crk. (UCB); Pine Mdw. (UCR); Pinyon Flat (UCB); Ribbonwood (UCB, UCR); Vandevanter Flat (UCB). San Diego Co.: 5 mi N Borrego Spgs. (UCB); Boulevard (KU, SDNH); Campo (KU); Oak Grove (UCB); 7.7 mi S Oak Grove (UCR). Collection dates are from May 21 to November 1. Males and females have been collected at light.

*Etymology.* Named for the genus of its host plant, *Adenostoma sparsifolium* (ribbon bush or red shank; Rosaceae).

*Discussion.* This species is distributed in the chaparral region of Los Angeles, Riverside, and San Diego counties, California. It is the only plant bug (Miridae) other than *Rhinacloa forticornis* Reuter that breeds on *A. sparsifolium*, and appears to have more than a single generation per season (J. D. Pinto, pers. comm.). The distribution of *sparsifolium* is reported (Munz and Keck, 1973) to extend into San Luis Obispo and Santa Barbara counties, but *adenostomae* has not been collected north of Mint Canyon in Los Angeles County.

*Phytocoris adenostomae* closely resembles *P. acaciae* Knight, 1925, *P. miniatus* Knight, 1961, and *P. occidentalis* Stonedahl, 1984, but is distinguished from these species by the dark bristle-like setae on the first antennal segment and the broad, densely setose genital tubercle of the male.

## ACKNOWLEDGMENTS

I wish to thank Michael D. Schwartz and John D. Pinto for critically reviewing the manuscript, and Beatrice Brewster for clerical assistance. The following institutions and curators kindly loaned specimens for study: Snow Entomological Museum, Lawrence, Kansas (KU), Dr. George W. Byers; San Diego Natural History Museum, California (SDNH), Mr. David K. Faulkner; University of California, Berkeley (UCB), Dr. Jerry A. Powell; University of California, Riverside (UCR), Mr. Saul I. Frommer and Dr. John D. Pinto. This work was partially supported by a grant from the Theodore Roosevelt Memorial Fund, American Museum of Natural History, New York.

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## NOTES AND COMMENTS

### NEW WATER MITE (PROSTIGMATA: PARASITENGONA)—CHIRONOMID (DIPTERA) ASSOCIATIONS FROM OTSEGO LAKE, NEW YORK

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Water mites complete six stages during their development. They are the egg, larva, nymphochrysalis (or protonymph), deutonymph, imagochrysalis (or tritonymph) and adult. The active post-larval instars, the deutonymphs and adults, are usually free-living forms which feed upon crustacea, small immature insects and insect eggs. In the majority of mites with known life histories, the larvae selectively seek out and attach to insects that serve as appropriate hosts. Documented hosts include members of the orders Hemiptera, Odonata, Coleoptera, Trichoptera and Diptera, especially of the family Chironomidae. These insect hosts provide nutrition for further development as well as an efficient mode of dispersal.

During a study of the mussel parasite, *Najadicola ingens* (Koenike) (Hygrobatoidae: Pionidae) in Otsego Lake, New York (Simmons and Smith, 1984), 3,239 aquatic insect imagoes were examined for parasitic mites. The chironomid, *Ablabesmyia annulata* (Pentaneurini), constituted 83.5% of the total studied. Mite larvae belonging to the genus *Arrenurus* were removed from 26.5% of the midges of this species. They were located on the postero-ventral region of the thorax and on the ventral surfaces of the 1st and 2nd abdominal segments. In addition to members of the genus *Arrenurus*, mites of 12 other genera were identified on midges from a variety of chironomid genera.

These samples revealed eight new associations not previously reported by Smith and Oliver (1976), or in more recent literature. The following is a list of the new associations with the number of parasitized chironomid individuals from each genus indicated in parentheses: *Hydrodroma* (Hydrodromidae) from *Ablabesmyia* (Pentaneurini) (4); *Oxus* (Oxidae) from *Paratendipes* (Chironomini) (1); *Limnesia* (Limnesiidae) from *Cladopelma* (Chironomini) (1); *Unionicola* (Unionicolidae) from *Tribelos* (Chironomini) (1); *Piona* (Pionidae) from *Tribelos* (1); *Wettina* (Pionidae) from *Paralauterborniella* (Chironomini) (1); and *Forelia* (Pionidae) from *Cladopelma* (1), and *Tribelos* (1).

The determinations were left at the generic level due to the difficulty of identifying mite larvae to species without undertaking rearing experiments. Although these associations are new and have not been previously reported, none of them are unexpected in that larvae from these mite genera were known to parasitize midges from genera closely related to those listed here.

The author would like to thank Mr. Joseph Fagnani, Division of Laboratories and Research, New York State Department of Health, Albany, New York for identifying the chironomid genera, and Dr. Ian M. Smith, Biosystematics Research Institute, Agriculture Canada, Ottawa, Canada for identification of the mite larvae and for review of this manuscript.—Thomas W. Simmons, Biology Department, State Uni-



*versity College of New York at Oneonta 13126. (Present address: Department of Biological Sciences, St. John's University, Jamaica, New York 11439.)*

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## BOOK REVIEWS

*J. New York Entomol. Soc.* 93(4):1277–1278, 1985

**Escarabajos. 200 Millones Años de Evolución.**—Miguel Angel Morón Ríos. 1984. Publication 14, Instituto de Ecología, Mexico, D.F. 132 pp. \$40.00. Available from: Instituto de Ecología (attn: Patricia Reidl), Apartado Postal 18-845, Delegación Miguel Hidalgo, 11800 Mexico, D.F., Mexico.

By the sacred scarab, *another* good book about scarabs from the folks at the Institute of Ecology in Mexico City (see also Halfpeter and Edmonds, 1982, with review by Ratcliffe, 1984). This book, however, is a bit more unusual than many that are reviewed in these pages inasmuch as it is written for a general audience; it is not a scientific treatment in the sense that it is not a technical volume targeted for scarab systematists. Rather, it is a marvelous example of science expertly distilled for presentation to the general public or to scientists other than entomologists. The slip cover indicates the book is directed to the public and that it will be used by teachers and students at intermediate and higher levels. This should be especially true because of the book's informative and synoptic review of a large and popular group of beetles, namely Scarabaeoidea. The author is well qualified to handle the subject because of his years of research and publications dealing with these animals and, most recently, because of his extensive efforts in putting together an excellent interpretive display on scarabs at the Museo de Historia Natural de la Ciudad de Mexico.

The chapters are entitled (1) Morfología, (2) Diversidad y Hábitos, (3) Importancia y Utilidad, (4) Colecciones y Estudio, (5) Clasificación General, and (6) Literatura Citada. A prologue, introduction, recommended reading, glossary, and general index are also included.

The first chapter asks, What is a scarab? Scarabs are then defined and distinguished from other Coleoptera. A concise narrative and illustrated overview is provided dealing with scarab body structure, both external and internal. A brief discussion follows on form and color that is supplemented by many beautiful photographs. Size and relative strength are reviewed, and a commentary on the possible functions of horns (possessed by so many of these beetles) is given.

The second chapter relates to diversity and the habits of scarabs. Morón states that there are about 35,000 species of Scarabaeidae, and that perhaps as many as 70,000 species will be ultimately described. He notes that there are about 1,300 species in 160 genera in Mexico. The large variety of habitats where these insects live (ranging from desert to tropical forests, lowlands to high mountains) is described as well as what they eat and how they reproduce. Brief, synoptic life histories are given for *Goliathus orientalis* Moser, *Canthon humectus* Say, *Proculus mnischevi* Kaup, *Megasoma elephas* (Fabr.), and *Phanaeus mexicanus* Harold.

The third chapter delves into the importance and usefulness of scarabs to man. Agricultural importance, mostly as it pertains to the pest status of some species, is briefly mentioned. The benefits of adult scarabs and their larvae to the decomposition of dead timber in forests and to the recycling of dung in cattle pastures is highlighted, and mention is made of the ecological importance and relationships between organisms (both plant and animal) as they relate to scarabs.

Chapter four is concerned with collecting and studying scarabs. It is accurate and up to date and will prove especially useful to beginners who have little experience with collecting methods or the different types of insect collections. Many useful diagrams are included on trapping insects and preparing specimens for a collection.

The fifth chapter provides a schematic, general classification of arthropods. The classification is more detailed for the Scarabaeoidea (down to subtribe where applicable). Morón chose to recognize five families of scarabaeoids (Lucanidae, Passalidae, Trogidae, Melolonthidae, and Scarabaeidae) following the usage of Endrödi (1966). This is contrary to the view held by most North American workers who recognize only Passalidae, Lucanidae, and Scarabaeidae. This digression into the old European school of extensive splitting and elevation in rank of subfamilies is my principal, albeit minor, objection to the contents of this book. Each of the scarabaeoid families and subfamilies is then characterized by Morón as to form, numbers, distribution, and habits with a concluding comment on how many species of each particular taxon occur in Mexico. All of these synopses are accompanied by excellent habitus drawings and illustrations of various body structures.

The last chapter consists of the literature cited. It was not intended to be a complete review or even synoptic in nature, but it is a very good introduction to the kinds of publications available about Scarabaeidae. This should be particularly useful to non-specialists desiring a broad overview and who may be wondering where to start in familiarizing themselves with the scarab literature.

There are 174 figures in the book, and an impressive 92 of them are in color. Many of the fine line drawings were completed by the author himself, and all the illustrations are excellent. The visual effect of the entire book is extremely pleasing due, in part, to the effective layout design by Rebeca Cerda González. The volume is nicely produced on good paper although I believe the binding could have been more closely sewn based on the copies I have seen. Considering its moderate size and target audience, the book seems slightly overpriced, but perhaps the large number of color pictures negates that particular criticism.

I found very little technically at fault with the contents of the book. The specimens identified in figure 50 as *Chiasognathus granti* are misidentified, figure 124 was printed upside-down (probably inadvertently), and the citation for figure 161 was not included in the literature cited. Otherwise, the book is genuinely informative, current, and scientifically accurate.

I enthusiastically endorse and recommend this book to anyone interested in beetles. Those interested especially in Scarabaeidae, whether amateur or professional, should seriously consider obtaining it. The book is in Spanish.—Brett C. Ratcliffe, *Systematics Research Collections, W436 Nebraska Hall, University of Nebraska State Museum, Lincoln, Nebraska 68588-0514*.

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**The Spiders of Great Britain and Ireland.**—Michael J. Roberts. 1985. Harley Books, Martins, Great Horkesley, Colchester, Essex CO6 4AH, England. Volume 1 (*Atypidae*—*Theridiosomatidae*), 229 pp., £45.00; Volume 3 (Colour Plates), 256 pp., £55.50 (combined price for Volumes 1 and 3, £85.00).

For spiders, as for many other groups of arthropods, a page of illustrations often provides more useful taxonomic information than could a dozen pages of text. Most significant works on spider taxonomy are consulted as much for their figures as for their other content (Simon's classic *Histoire Naturelle des Araignées*, published between 1892 and 1903, and covering the world fauna at the generic level, is one of the few obvious exceptions). Roberts' projected three-volume series on British spiders, of which Volumes 1 and 3 are now available, exemplifies the pattern: illustrations are its *raison d'être*.

Volume 3 consists of 237 full page, large format, color plates; most pages are devoted to a dorsal view of a single spider, accompanied by a line sketch showing the actual size of the specimen. About 30 plates depict four specimens instead of one, and in these cases the legs are indicated only by outline sketches of their more proximal segments. The fineness of detail is unsurpassed in the existing literature. From the first plate, a magnificent painting of *Atypus* (the only British mygalomorph, or tarantula-like, spider), through the deep reds of *Dysdera*, the delicate tans of *Psilochorus*, and the vibrant greens of *Micrommata* and *Diaea*, colors and patterns are meticulously rendered and lovingly reproduced. Only a superbly talented artist who is also a practiced arachnologist could have produced these portraits; remarkably, the volumes were executed while their author was a medical student and practicing physician. The long British tradition of distinguished amateur natural history is evidently quite alive, and Roberts' graphic demonstration of the beauty of spiders might even lure some of his colleagues away from the butterflies and beetles!

The first two volumes (the second, on the Linyphiidae, is scheduled to appear in 1986) contain an account of the spider species recorded from Britain and Ireland, accompanied by detailed (mostly black and white) illustrations of male and female reproductive organs. As Roberts notes, "The nature of this book means inevitably that it is concerned mainly with corpses and genitalia." The genitalic figures amply meet his stated goal of making "the identification of British spiders a little easier." Interestingly, Roberts comments (pp. 26–27) that

When comparing the male palp or epigyne of a specimen with the illustrations in this book, one should get into the habit of looking at the *whole structure*. Most people will have seen the paired cartoons in newspapers where one differs from the other and the reader has to 'spot the differences'; the perceptive approach needed for this is also the best approach when examining spider genitalia. In many works which illustrate spider palps, only a part of the structure is shown, or the reader's attention is directed to one particular aspect of the organ as being *the* diagnostic feature. Whilst this may in the short term sometimes be helpful, and occasionally is necessary, it can be misleading and discourage observation of other structures. As it is, many experienced arachnologists, when identifying specimens, spend their time looking at palps and epigynes and scarcely look at the whole animal. If taken a stage further one can be led into just looking at the tibial

apophyses of the palp in one genus, or the conductors in another. In this situation, any new species cropping up may be missed if the differences in its palpal structure do not occur in the appropriate conventional diagnostic area.

Given this concern, it is most perplexing that Roberts follows Locket and Millidge's *British Spiders* in providing, for the males of many genera, only a retrolateral view of the palp. Most details of palpal structure can be observed only in ventral view; although retrolateral views may suffice to distinguish the (known) British species, they do not allow workers elsewhere to judge whether their specimens are conspecific with, or closely related to, British ones.

The systematic treatment is a mixture of traditional and modern elements, but Roberts does generally refer to recent works even when he opts to ignore their nomenclatural implications in his "compromise" classification. He recognizes such classical but artificial assemblages as the Cribellatae and Haplogynae (although the family Pholcidae is curiously removed, without comment, from the latter group). Also curious is the absence of references to many obviously diagnostic generic synapomorphies. For example, neither the keys, descriptions, nor illustrations indicate that specimens of *Gnaphosa* have a serrate cheliceral keel, that those of *Callilepis* have a cheliceral lamina, that zelotines (here lamentably lumped into a single genus) have preening combs on metatarsi III and IV, or that an abdominal stridulatory file characterizes *Antistea*. But such information is available elsewhere, and Roberts' artwork is not. All spider enthusiasts will want the entire set, and aficionados of fine natural history illustration should snatch up Volume 3.—*Norman I. Platnick, Department of Entomology, American Museum of Natural History, New York, New York 10024.*

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**Population Biology and Evolution.**—K. Wohrmann and V. Loeschcke (eds.). 1984. Springer-Verlag, Berlin. 270 pp. \$40.00.

In the early to mid 1960's attempts were being made to bring together ecology, population genetics, and developmental biology to form a unified field of evolutionary biology. One of the most important works to come out of this period was *Population Biology and Evolution*, the proceedings of a symposium held in 1967. Just the year before, however, the electrophoretic bomb had been dropped, and we all know what happened: for at least a decade the primary aim of evolutionary biology became the melding of electrophoretically-determined allele frequencies with the models of theoretical population genetics. Although electrophoresis has provided invaluable information on taxonomic questions, population structure, breeding systems, and so on, it has not, in my opinion, shed much light on the question it was initially supposed to answer: What is the genetic basis of evolutionary change? To answer this question, one must focus on phenotypes—how they are produced and how selection acts on them. Thus, we have another volume, the proceedings of a symposium held in 1983, entitled *Population Biology and Evolution*, whose stated goal is to determine how population genetics and evolutionary ecology can be unified. The book is divided into eight sections: genotype and phenotype, quantitative characters and selection in natural populations, theoretical aspects of density regulation and life histories, genetic



heterogeneity and ecological factors, genetic structure and demography in plants, population differentiation and asexual reproduction, theoretical aspects of coevolution, and comments on models. What emerges from this diversity of papers is that the phenotype, hidden for so long behind a veil of acrylamide and starch, is indeed an object worthy of attention.

Most of the papers in this collection are adequate, but not outstanding; the standouts are the chapters by Prout, who shows that censuses of adults alone are not sufficient for understanding population dynamics, and by Shapiro, who presents some very interesting data on the genetic and environmental contributions to phenotypic variation in butterflies. In general, however, the present volume does not measure up to its predecessor, to which no mention is ever made; it will not convince neophytes that populations can be as interesting as restriction-enzyme digests. But the sixties were halcyon days. Today, evolutionary biology is seen by some to be floundering, unsure of direction. (Plant population biology, due in large part to the inspired leadership of John Harper, is a notable exception.) But if we are to make progress, then the study of phenotypes and populations must be added to the study of genes. The present volume could be profitably perused to see where we might be going.—*John Jaenike, Department of Biology, University of Rochester, Rochester, New York 14627.*

*J. New York Entomol. Soc.* 93(4):1281–1285, 1985

**Chemical Ecology of Insects.**—W. J. Bell and R. T. Cardé (eds.). 1984. Chapman and Hall, London. 524 pp. Distributed in U.S. by Sinauer Associates, Sunderland, Massachusetts. \$28.50 paper, \$45.00 cloth.

As a recognizable field of study, chemical ecology is scarcely more than 15 years old. The past few years, however, have seen the formation of the International Society of Chemical Ecology and a great acceleration in the rate of appearance of original research papers, reviews, and books concerned with the role of chemicals in ecological interactions.

The arrival of any new symposium volume or edited collection must be regarded with decidedly mixed emotions by individuals or libraries with limited budgets. Happily, I can recommend this book to anyone working in insect behavior or ecology, without serious reservations about its cost or content. The editors have largely succeeded in their goal of covering all major aspects of the chemical ecology of insects. The only conspicuous omission is insect defensive chemistry; the book by Blum (1981) provides the most recent survey of that topic.

Other recent books that cover similar ground include those edited by Futuyma and Slatkin (1983), Denno and McClure (1983), Ahmad (1983), and Nordlund et al. (1981).

Of these, the volume edited by Nordlund et al. overlaps most extensively with the present volume, though its emphasis is on applications for pest management. A second difference between these books concerns terminology. In general, the contributors to "Chemical Ecology of Insects" have chosen to use practical, functional terminology in preference to latin or greek constructions. In the opinion of this reviewer, it is an encouraging development. Chemical ecology as a discipline cannot become divorced from other fields of behavioral and ecological research. The ad-

vantage of a neat, comprehensive classificatory scheme for chemical communication and defense systems (semiochemicals vs. allelochemicals; allomones, kairomones, synomones, etc.) is purchased at the price of erecting barriers to communication with workers from other fields of entomology, behavior and ecology.

Precise categorization also brings the risk of emphasizing classification over description of the actual behaviors. Bell, in his chapter, makes this point strongly with respect to analyses of orientation behavior. Too frequently, attempts to categorize orientation behaviors as klinotaxes, tropotaxes, etc., have obscured the fact that individual insects are capable of using multiple orientation strategies in different circumstances.

In the first chapters, Städler (contact chemoreception) and Mustaparta (olfaction) review the physiology of insect chemoreceptors. Both reviews emphasize the still primitive state of present knowledge about the neurophysiology of chemoreception. One generalization emerging from current research is that perception of pheromones is dominated by receptors specifically tuned to particular chemicals ("labelled line systems"). Perception of host-plant chemicals, in contrast, appears to involve generalized receptors, and identification of hosts occurs by central nervous system integration of complex stimuli from several different receptors ("across-fiber patterning").

Elkinton and Cardé present an excellent review of the biophysics of odor dispersion. They emphasize the inadequacy of the simple (but widely used) analytical models for odor plume behavior under natural field conditions. They question the potential for insects to use a concentration gradient (klinotaxis) for orientation to an odor source under field conditions at significant distances (greater than 1 m). The vagaries of plume dispersal suggest that odor cues may contain only limited information about resource quality or abundance.

Bell (chemo-orientation in walking insects) suggests that chemical cues may serve primarily for initiation of search behavior, and may provide only general information on odor plume boundaries. Cardé (chemo-orientation in flying insects) supports the general consensus that upwind flight initiated by odor perception (upwind anemotaxis) is the primary mechanism of orientation, yet emphasizes that the details of the mechanism are still unclear. However, under conditions when only chemical cues are available, insects may be able to use instantaneous and temporal comparisons to follow a concentration gradient to an odor source. Insects are undoubtedly responsive to multiple cues (visual as well as chemical) and have the potential for using several systems simultaneously or sequentially. A major area for further research concerns the integration of multiple sensory modes in orientation responses.

Miller and Strickler (finding and accepting host plants) provide an excellent, clearly written, review of host location in phytophagous insects. Despite its brevity, their chapter is comprehensive and remarkably free of taxonomic provincialism. It is the best available introduction to the subject, and should be read by anyone studying insect/plant interactions. In the companion chapter, Scriber (host-plant suitability) discusses the importance of plant nitrogen, water and allelochemicals (toxins) in determining the growth and survival of an insect, once it has located a host plant. Scriber argues that nitrogen and water content of plant tissues define a maximum potential for growth rates and efficiencies; the occurrence and concentration of allelochemicals depress performance below this potential. Ecological and evolutionary

hypotheses about feeding specialization must be evaluated with respect to this potential, and with regard to the possibility of intraspecific variation among populations of generalized feeders.

Vinson (parasitoid-host relationships) and Prokopy, Roitberg, and Averill (chemically-mediated spacing) offer straightforward reviews of their subjects. Much of the material they present here has been reviewed by these authors elsewhere (in Nordlund et al. 1983, and various Annual Review volumes). Vinson briefly summarizes the role of chemical cues in host location by parasitoid insects, and the means by which they overcome host resistance and subvert host developmental and endocrine processes. Prokopy et al. focus on pheromones which serve to reduce crowding, or signal previously-searched sites to ovipositing females.

In an interesting chapter, Nault and Phelan discuss alarm and aggregation pheromones in presocial insects (aphids and membracids). They argue that the evolution of these pheromone systems (and associated morphology) followed the development of group-living in presocial insects. The behavioral responses to the pheromones are highly variable among (and within) taxa in response to selection imposed by degree of aggregation, presence of ant attendants, and the risks associated with various forms of escape response. The evolutionary- and coevolutionary-dynamics of these systems represent a potentially fertile area for research.

Huheey discusses mimicry in a good, general review that focusses primarily on theoretical and conceptual issues. He provides a sensible guide to several controversial aspects of the subject (toxicity vs. distastefulness in predator learning; the relationship between abundance and palatability of models and mimics). He offers a complementary perspective to that of Gilbert in Futuyma and Slatkin (1983). It is apparent that mimicry systems continue to offer possibilities for work in ecological genetics, especially with the integration of quantitative chemical analyses to address questions of inter- and intra-specific variation in palatability of models and mimics.

Birch covers aggregation in bark beetles in a selective review focussing on species attacking ponderosa pine in California. Birch manages to present a coherent sketch of bark beetle chemical communication, without avoiding the complexities, or the differences that occur among various species and genera in different regions. The availability of abundant terpenoid compounds in host trees has supplied the raw material for elaboration of a highly developed chemical language among the bark beetles. Multiple species interactions involving competitors, predators, and parasites are involved in the responses to aggregation pheromones. There is a great potential for coevolution involving these communication systems, and Birch presents some intriguing examples of inter- and intra-specific variation in pheromone blends and responses.

Cardé and Baker examine sex pheromones in insects from the perspective of general ecological and evolutionary thought. Emphasizing lepidopteran pheromones, they discuss character displacement in chemical signalling systems, and the possibility of speciation by means of shifts in pheromone production and response. Their discussion is limited by the lack of adequate information on the extent of natural variation among populations of single species, and on the genetic basis of pheromone production and response. Conclusions about the evolution of sex pheromone systems, and their potential role in speciation are still premature.

The concluding chapters consider the chemical ecology of bees (Duffield, Wheeler

and Eickwort), ants (Bradshaw and Howse), and termites (Howse). The chapters differ in their emphases, reflecting both differences in the roles played by chemicals in each taxon, and differences in the state of knowledge about each group. In the bee chapter, Duffield et al. present a comprehensive catalogue of pheromones and other exocrine compounds, organized taxonomically and by glandular source. The functions of many of these compounds are uncertain. As the authors note, research on the behavioral role played by these bee chemicals lags far behind their chemical identification.

In contrast, the identity and involvement of pheromones in the behavior and ecology of ants is well established. The present state of knowledge permits Bradshaw and Howse to organize their chapter according to function: alarm and defense; aggression and competition; recruitment and foraging. Their review is balanced and thorough.

The past 10 years has seen a virtual explosion of new information on the defensive chemistry of termites. Termite chemicals used in defense have proved to be a happy hunting ground for natural products chemists in quest of novel structures, and provide data relevant to questions of termite systematics. Much of the substance of this chapter is duplicated in two recent (and excellent) reviews by Prestwich (1983, 1984). Knowledge of termite pheromones still lags far behind that on ants, however, largely because colonies are difficult to manage or study in the laboratory. Another area needing study is the ecology of termite defenses. Howse suggests that ants and other invertebrate predators which feed on termites may require specific detoxication or avoidance mechanisms to overcome their prey, and may be highly specialized predators as a consequence. This raises the possibility of an intimate coevolution among termite predators and prey that has yet to be carefully investigated.

Comparison of "Chemical Ecology of Insects" with the pioneering "Chemical Ecology" (Sondheimer and Simeone, 1970) illustrates the growth in the field during the past 15 years. The range and extent of knowledge has vastly increased, but the general direction of research has shifted as well. The identification of chemicals used in communication or antagonistic interactions is no longer the main challenge. The message in the present volume is that the greatest need now is for integration of chemical knowledge into an understanding of ecological interactions. Field studies are essential for further progress, as well as research on the genetic and physiological bases of production and perception of chemicals.

One possible danger lurking in the formal establishment of a distinct discipline of chemical ecology lies in the tendency of practitioners in any field to communicate primarily among themselves. The impression one gets from this volume is that any such tendency among researchers in chemical ecology would be very unfortunate. In many chapters, the authors emphasize the inadequacy of considering chemicals in isolation for either communication or defense. Orientation behaviors in particular usually involve visual cues, as well as perception of often complex mixtures of compounds. It is apparent from most chapters that the most exciting directions for future research lie in the integration of chemical investigations with "traditional" behavioral and ecological research: chemical ecology with the emphasis on ecology. Investigation of intra-specific variation in the production and perception of chemical signals is also a key area for work; and a prerequisite, along with genetic studies, to an understanding of the evolution of chemical communication and defense in in-



sects.—Robert H. Hagen, *Section of Ecology and Systematics, Corson Hall, Cornell University, Ithaca, New York 14853.*

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**Courtship Behaviors of the Hawaiian Picture-winged *Drosophila*.**—Herman T. Spieth. 1984. University of California Publications in Entomology, Vol. 103. vii + 92 pp. \$9.50.

The picture-winged species-group members, as implied by their name, are the most impressive Hawaiian *Drosophilidae*. This is only one of ten species-groups erected for Hawaiian *Drosophila*, but comprises about one-quarter of the species. The group has been a favorite of many evolutionary biologists because of their modifications, which include lekking and very complex courtships. Here Spieth adds to our knowledge an impressive amount of previously ignored behavioral information. Despite what I feel to be major conceptual and some methodological flaws in this publication and in the companion paper (Spieth, 1982), the work is still of lasting significance.

Spieth's work views with work on Hymenoptera sociality as the most thorough behavioral analysis devoted to the study of insect evolutionary relationships. My perusal of the work uncovered 57 behavioral elements (fixed-action-patterns in ethological jargon), 53 of which are employed by the male flies for female sexual stimulation. Some elements are so distinct (i.e., anal droplet pulsation, and the manner of wing semaphoring) that there is little question of their homology in different phases of the same fly's courtship as well as among species. This, and the fact that various combinations of element sequences are performed, makes the taxonomic value of the characters obvious. In fact, Spieth comes to some substantial taxonomic conclusions. For example, the various affinities of *Drosophila neoperkinsi* and of *D. differens* are confirmed by their behaviors. The reluctance to revise the classification of some flies, however, is disconcerting. Four instances are obvious where Spieth is content with *status quo* even though blatant behavioral evidence contradicts the standard taxonomy: *Drosophila picticornis* is deemed a relictual species having affinities with



almost all other members of the whole species-group, but it is kept as a member of the *planitibia* subgroup. Also, *Drosophila conspicua* is kept as a *pilimana* subgroup member even though (p. 57) "it rationally can be considered the founder and at present the sole member of a new, unnamed species-subgroup of the picture-winged flies."

Cladistic practitioners will have plenty to sink their teeth into here. On one hand, the work does appear phylogenetic since hierarchical groups are supported and some even devised, the amount by which they are divided depending on character variability and number. Also, taxon sizes are disparate so as to emphasize relationships (but not entirely, as I mentioned earlier) and not taxonomic convenience. Implicit throughout is a dependence in reconstructing phylogeny not on the discovery of ghost taxa, but of new characters. However, paraphyletic groups are the rule rather than exception, probably because Spieth has a phenomenal assurance in identifying ancestors that is almost eerie. *Drosophila macrothrix*, for instance, is explained as (p. 49) "probably the founder of a new species-group sometime in the future if it should provide immigrants to other islands." The 1982 paper in particular is riddled with very extensive discourse on ancestors and, frankly, all of it is supported by no more explicit reasons than statements like "behavioral and chromosomal evidence indicate that [x] evolved out of [y]." These methods are probably the reason why the characters used to support the existence of the *adiastola* species-subgroup (i.e., hypertrophied male labellar "setae") are also those that define the modified-mouthparts *species-group*. Evolutionary biologists, beware.

Considering the current rage among evolutionary biologists (i.e., Bateson, 1983), it is a boost to know that female choice really does seem to be at work in the cladogenesis of these flies. Of the 71 male courtships that were analyzed, only for 10 of the species were they indistinguishable. Females of most species were found to be passively motionless during courtship and usually responded, if receptive, simply by extruding the oviscapae. Most often females were unresponsive to male overtures. Besides the fact that stimulation of the female appears to be the main selection pressure in sexual elaboration, Spieth mentioned on the last page—but provides no data—that most females in nature eventually become mated since most are inseminated. "How much is most?" can be a very important consideration. Based on Spieth's data, I dare say that sexual behavior seems to have evolved much faster than morphology, proteins, the use of larval breeding sites, and even chromosome structure. It is a pity that no mention is made in either publication of recent ideas on directional mate choice in relation to the direction of phylogeny (reviewed in Giddings and Templeton, 1983), a topic introduced by Kaneshiro's work on these very same flies. Other relevant papers that were not addressed are Ringo (1977) and Templeton (1979), as well as several classics.

To really appreciate this work the 1982 paper must be read. This monograph is difficult to wade through since it is 90% species courtship descriptions, with a synthesis of the behavioral, biogeographic, karyotypic, and breeding site information in the 1982 paper. Inexcusable on the part of the author and editors is that most of the review portions of the monograph reiterate, verbatim for some paragraphs, parts of the 1982 paper. Why both publications were not published as one monograph is beyond me. On par for the Hawaiian drosophilidologists, except for D. Elmo Hardy,

is a distressing lack of suitable illustrations. The monograph has only 5 line drawings, all of which are also in the companion paper. Figure 1 is actually quite awkward: it should be labelled as the labellum instead of "mouthparts" for the sake of precision, and is better interpreted when pointing left rather than up. This lineage of flies is certainly among the most bizarre in Acalypttratae Diptera, but the illustrations and morphological interpretations do not bear that out. For instance, the hypertrophied "setae" on the labellum of some species are probably prestomal teeth, which are modifications of the pseudotracheae. The meanings of some terms are vague. Not until page 35 will the reader discover that "HUW" posture mentioned in the previous descriptions is the Head Under Wing posture. Wing "vanes" are the blades; "anal papilla" is the cercus; and the manner of semaphoring (deliberate wing motions, as a flagman makes when signalling) should be made explicit. I suspect that when "drosophiloids" of Hawaii are mentioned, reference is made actually to just drosophilids since other families in the superfamily (Camillidae, Curtonotidae, Diastatidae, Ephyridae) are virtually untreated for Hawaii. Relevant papers not mentioned in either of the two publications are Craddock (1974) on higher relationships, Kaneshiro (1976) on the *planitibia* species-subgroup, and Ohta (1978) on the *grimshawi* species-subgroup.

I have been very critical here because for no other group where adaptive radiation is discussed are the Hawaiian Drosophilidae surpassed in popularity. It is essential that all the details be exact. However, the data in this monograph really is the tip of an iceberg. When culturing methods are devised for most of the species, behavioral geneticists will be able to fine tune the analysis, perhaps down to the level of identifying the neuromuscular channels and genes underlying the sexual fixed-action-patterns. Whether or not that future work (and the recombinant DNA work that will surely ensue) will corroborate Spieths' decisions on behavioral homologies and phylogeny is not most at issue; the fact remains that his observations stimulate questions and lay foundations.—David Grimaldi, Department of Entomology, Cornell University, Ithaca, New York 14853.

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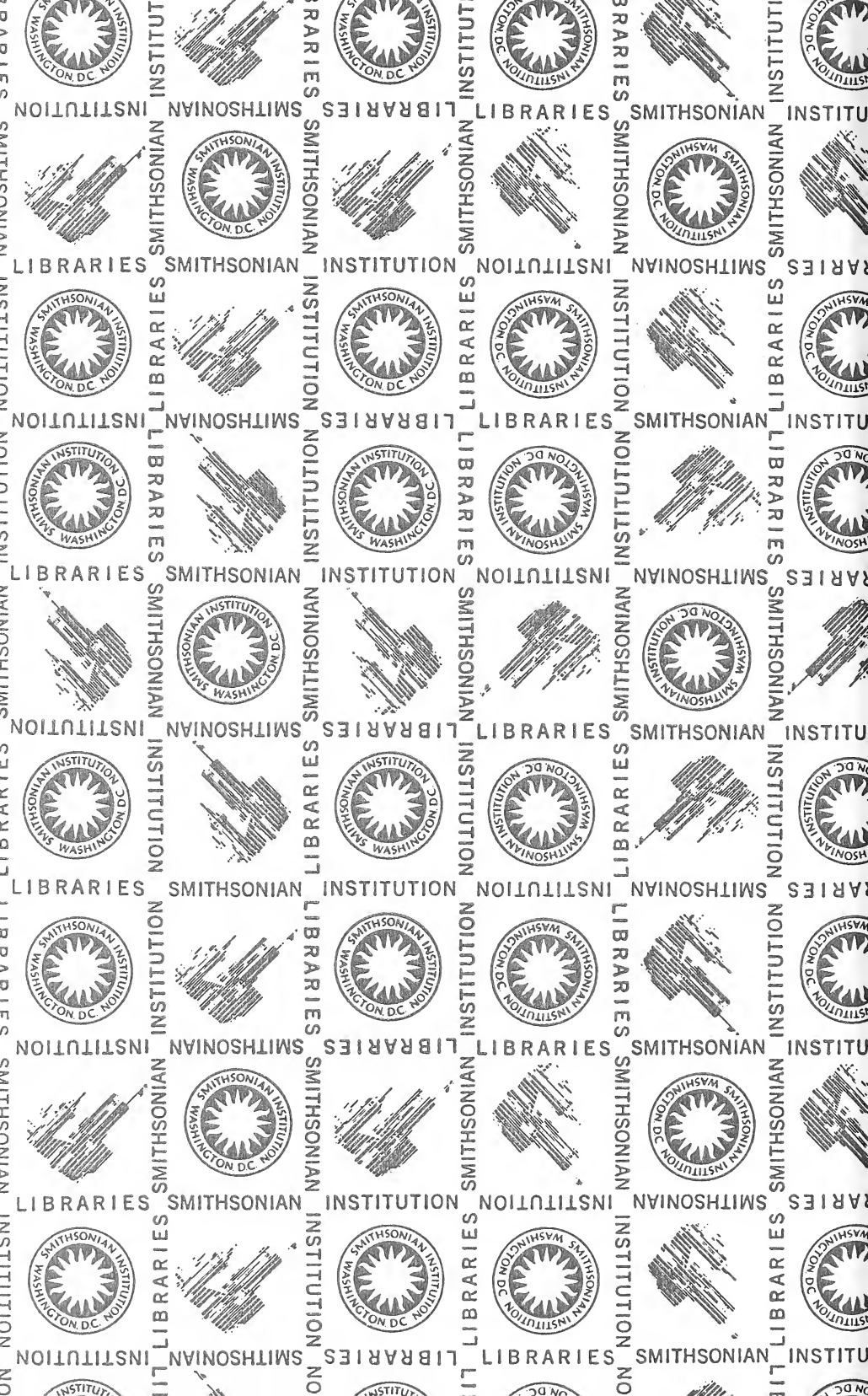
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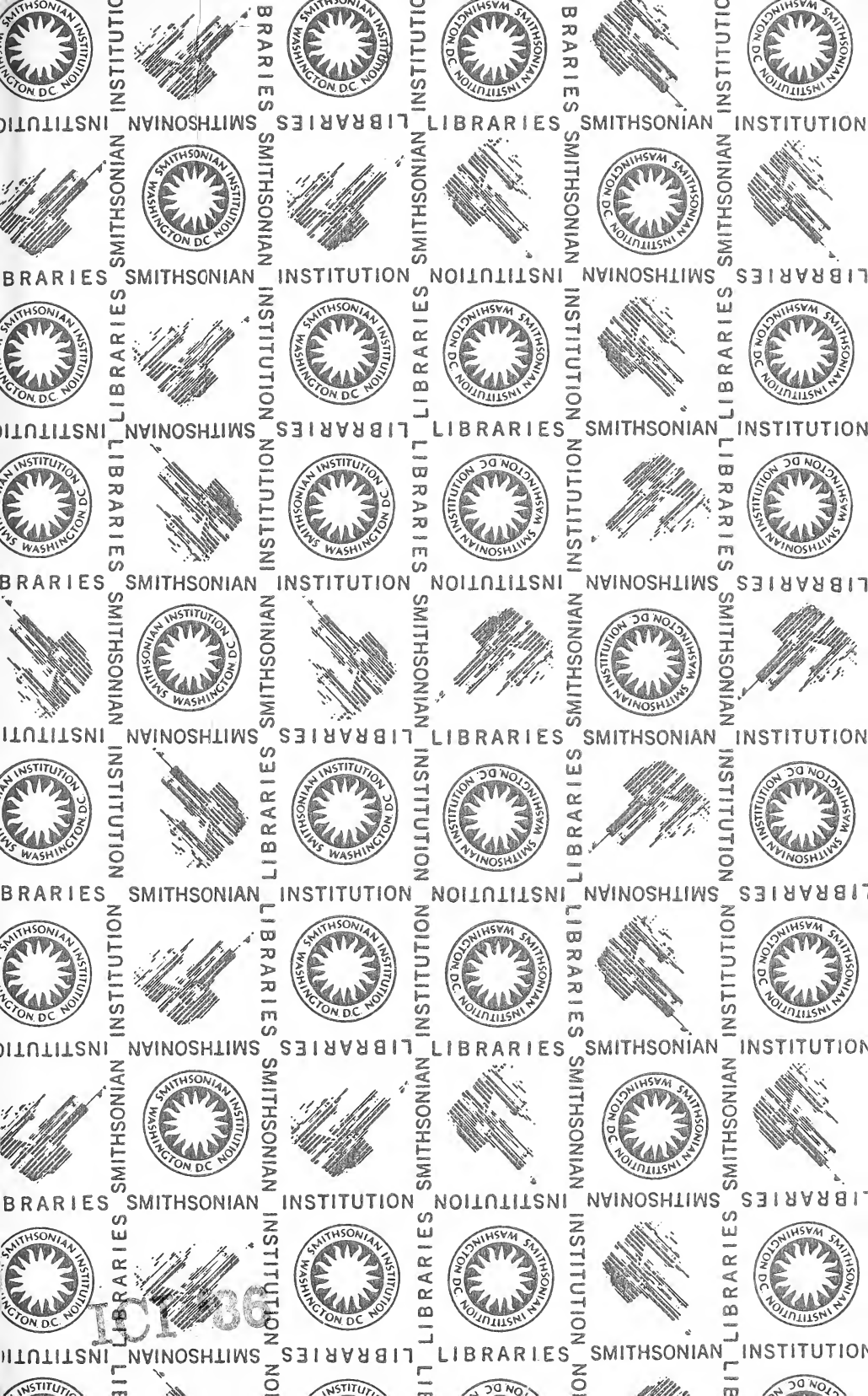














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